UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS
DEPARTAMENTO DE FÍSICA

Electrophysiological signatures of event segmentation during movie viewing and recall

Marta Marques de Almeida e Silva

Mestrado Integrado em Engenharia Biomédica e Biofísica
Perfil em Sinais e Imagens Médicas

Dissertação orientada por:
Prof. Lluís Fuentemilla Garriga
Prof. Alexandre Andrade

2018

Acknowledgements

I would like to start this thesis report by thanking everyone who made this project possible and helped me throughout its development.

First of all, I would like to thank Professor Lluis Fuentemilla for giving me the opportunity to be a part of an amazing research group. His support and encouragement was fundamental for my development as a scientist. His excitement and love towards the world of neurosciences it's truly contagious and made me want to pursue a path in this world even more. I also need to thank him for doing more than a thesis supervisor would be expected to and giving me opportunities to attend conferences, write a paper and opening the door to future collaborations. He made me feel like I was adding something to the team.

The crucial role of Professor Alexandre Andrade should also be acknowledge, who helped me during all the dissertation process, giving me support and valuable tips.

I would like to mention all the Brainvitge group for being so welcoming and making my day-to-day at the lab so pleasant. I would like to give a special thank to all my friends from the dynamics of memory formation group for supporting my work, helping me with it and cheering me up when I was feeling frustrated. Thank you for all the good moments and for being amazing friends and caring about me, even after my return to Portugal.

Thank you to my family for not only making this opportunity possible, but also for always being there for me. For calling, visiting and never stop believing and encouraging me to pursue my dreams.

A very special gratitude to João for being my best friend, always being there to cheer me up and make me stop doubting myself when there was no need. Thank you for being my biggest companion, making me feel at home and for inspiring me to work hard and never give up on my goals.

I also want to thank all my friends here from Portugal, specially Beatriz Simões and Diogo Cunha, for all the support and for always caring and making sure that I was doing well.

Lastly I want to express my gratitude to the Erasmus+ program for the scholarship they granted me with.

Abstract

Perception and memory have been widely studied in the context of discrete pictures or words. However, in real-life, we are faced with a continuous stream of perceptual input that arrive on a wide range of timescales. Previous studies have shown that our brain can segment this continuous stream of information into events that not only reveal a hierarchy from coarse to fine time-scales, but also integrate them differently throughout the cortex, with processing timescales increasing from tens of milliseconds in early sensory regions up to hundreds of seconds in higher-order regions. However, the neural mechanisms that support such event segmentation process during online encoding of a naturalistic and continuous experience remain unknown. To address this issue, we tested whether the formation of meaningful event models could be expressed by specific patterns of electrophysiological activity recorded from healthy humans elicited during the online encoding of a 50 minutes movie and if these patterns were predictive of participant's later memory recall of the encoded events during a free verbal and unguided recall test. Our results provide the first electrophysiological evidence for a memory related oscillatory signature of the event segmentation process. We found that, when facing a naturalistic continuous stimuli, our brain perceives the information in the form of discrete events which are stored in memory during a process that seems to occur approximately 400 ms after the end of each event and that is indeed predictive of later reinstatement of those events. This neural process suggests a possible congruency/incongruency evaluation mechanism which might represent the error-based updating mechanism, in which event models are updated at event boundaries in response to transient increases in prediction error, suggested by the *Event Segmentation Theory*. Our results also prove that naturalistic stimuli can be used in electroencephalography measurements, despite the natural limitations that arise with the use of such stimuli. In doing so we will be able to study, in a more ecological way, the mechanisms of memory formation during event segmentation.

Keywords: Electroencephalography, brain, memory, event segmentation, boundary.

Resumo

As memórias podem ser definidas como representações duradouras de eventos ocorridos no passado que se reflectem em pensamentos, experiências e comportamentos. Conscientemente ou não, elas são influenciadas pelo passado, necessárias para o nosso dia-a-dia e extremamente importantes no planeamento do nosso futuro. O armazenamento de memórias é feito por parte de inúmeras estruturas cerebrais pertencentes ao neocórtex - parte exterior do córtex - e pelo lobo temporal medial, onde podemos encontrar o hipocampo e seus tecidos envolventes. Estas duas regiões encontram-se em constante diálogo enquanto armazenamos e restabelecemos o fluxo de experiências diárias. Com base no estudo de lesões cerebrais nestas regiões, sabe-se hoje em dia que é possível dividir as memórias em diferentes categorias. As duas principais categorias são memória a curto prazo e a longo prazo. A primeira é responsável pelo armazenamento de informação temporariamente e se essa informação deve ou não ser transferida para a memória a longo prazo. Estas últimas são compostas por memórias conscientes e inconscientes, entre elas as memórias semânticas, episódicas e mais particularmente autobiográficas. Inicialmente as memórias são episódicas e armazenadas no hipocampo e com o tempo são transformadas em memórias semânticas no neocórtex.

Recentemente, uma nova linha de investigação tem se focado não na distribuição espacial do processo de armazenamento de memórias mas sim nas suas propriedades temporais e capacidade de distinguir informação que nos é apresentada com diferentes escalas temporais. Por exemplo, quando falamos ou lemos um texto, somos obrigados a identificar as diferentes sílabas para conseguir formar uma palavra, a perceber o sentido dessa palavra no contexto de uma frase, e uma frase no contexto de uma conversa. Não só temos a capacidade de segmentar a informação que percepcionamos mas também de nos lembrarmos desta informação na forma de episódios representativos das nossas experiências prévias. A primeira teoria formulada sobre este processo de segmentação toma o nome de *Event Segmentation Theory*. Nela a informação processada pelo nosso cérebro é representada por uma série de modelos de eventos, implementados durante rápidas alterações neuronais que ocorrem devido a um mecanismo de avaliação de predição do que deverá acontecer no seguimento de certa experiência. Esta alteração no erro de predição leva à segmentação da informação em diferentes eventos durante momentos a que se dá o nome de fronteiras. Desde a formulação desta teoria inúmeros estudos foram desenvolvidos com o intuito de compreender o funcionamento deste processo de segmentação. Estes estudos permitiram-nos obter provas de que a nossa actividade neuronal tem a capacidade de processar informação em diferentes escalas temporais, em diferentes regiões do cérebro. Zonas de processamento sensorial segmentam informação em eventos mais curtos, uma vez que os estímulos sensoriais são geralmente muito rápidos, e zonas de processamento elevado segmentam informação em eventos mais longos uma vez que têm de processar informação perceptual e cognitiva. No entanto, apenas recentemente começaram a surgir estudos que ligam este processo de segmentação à formação de memórias a longo prazo. Uma nova teoria, *Theory of Event Segmentation and Memory*, proposta o ano passado sugere que cada região cerebral processa informação na sua escala temporal preferida e que estes segmentos de informação são transmitidos de regiões que

processam informação a escalas temporais longas para o hipocampo, minutos após ser formada uma fronteira entre dois eventos. Ao ser activado, o hipocampo processa a informação do evento acabado de percepcionar e armazena a informação para que esta possa ser mais tarde reativada nas mesmas regiões de escala temporal longa. Após a formalização desta teoria uma série de outros estudos têm sugerido como principal responsável para a integração da informação de um evento na memória, a resposta neuronal que parece ocorrer durante as fronteiras entre eventos. No entanto, os mecanismos neuronais que suportam esta segmentação e integração na memória durante o processamento de experiências naturais e contínuas continuam por explicar.

Com o objetivo de explorar estes mecanismos, neste projeto testámos a possibilidade de a formação de modelos de eventos ser expressa por padrões eletrofisiológicos particulares a este processo. Para tal adquirimos dados de electroencefalograma (EEG) de 30 participantes saudáveis enquanto estes visualizavam 50 min de um filme. Para testar se o aparecimento de padrões neuronais específicos poderia ser preditivo de um correcto processo de memória pedimos aos participantes para, após a visualização do filme, relatar o que tinham acabado de ver de forma livre, mantendo a ordem em que a informação foi apresentada no filme e por quanto tempo conseguissem.

Os dados adquiridos foram pré-processados de forma a eliminar a maior quantidade de ruído possível e um modelo com a possível segmentação do filme em diferentes cenas foi construído com base em anotações de seis participantes externos. Após verificar que o sinal adquirido podia ser dividido nos eventos compostos pelo modelo construído este foi utilizado na primeira parte da análise em que o objectivo era avaliar o que se passava no interior dos eventos. Para tal os padrões neuronais adquiridos tanto durante a visualização do filme como durante o relato do mesmo foram comparados entre si para cada participante e comparados entre participantes. Verificámos que os padrões neuronais eram semelhantes entre participantes tanto para os dados obtidos durante a visualização do filme, em que o estímulo é o mesmo para todos os participantes, como para os dados adquiridos durante o relato, em que os participantes descrevem o filme de forma diferente. Apenas obtivemos elevados valores de semelhança entre os padrões do filme e o relato quando recorremos a um algoritmo de segmentação baseado em Hidden Markov Models para que a segmentação dos dados do relato fosse feita de forma individual para cada participante. Estes resultados permitem-nos concluir que o processo de armazenamento e restabelecimento de memórias é feito de forma semelhante e com base em eventos. Correlações entre diferentes propriedades dos eventos (duração do evento, ordenação dos eventos durante o relato, detalhes relatados em cada evento e autocorrelação do padrão neuronal de cada evento) e a precisão com o que filme é relatado para cada participante foram calculadas de forma a perceber se alguma destas propriedades poderia prever se um evento seria mais tarde relembrado durante o relato ou não. Apenas a duração do evento mostrou ser significativa o que indica que os processos que se desenvolvem durante a visualização de um evento não parecem ser decisivos para a sua integração na memória.

Após estudar o que se passava no interior de cada evento a nossa atenção voltou-se para as

fronteiras entre eventos. Para tal começámos por realizar uma análise de similaridade espaço-temporal (STPS) em que comparámos os padrões neuronais 5 s após as fronteiras com os 5 s antes das fronteiras e observámos que de facto existe uma alteração nos padrões neuronais quando uma fronteira ocorre, e que esta alteração não pode simplesmente ser explicada por uma distância temporal entre os dois eventos. Para observarmos então com mais distinção a resposta neuronal durante a fronteira, calculámos os *event related potentials* (ERPs), 2 s após cada fronteira, para todas as fronteiras e todos os participantes. Nestes, encontrámos uma clara distinção entre fronteiras correspondentes a eventos que não foram e que foram mais tarde relatados. A resposta neuronal dos eventos mais tarde relembrados está marcada pelo aparecimento do componente N400, conhecido por aparecer quando ocorre uma incongruência na informação a ser percepcionada. Estes resultados sugerem que, quando uma fronteira ocorre dá-se uma avaliação de congruência com a informação do evento passado e, quando mais incongruente for esta informação, melhor será armazenada na memória e mais tarde relembrada. Este mecanismo está de acordo com o mecanismo de avaliação de previsão proposto pela *Event Segmentation Theory*. Em suma os nossos resultados demonstram a existência de um padrão neuronal característico do processo de segmentação com aparecimento aproximadamente 400 ms após a formação de uma fronteira entre eventos, crucial para a correta integração desse evento na memória. Os nossos resultados provam também a validade de utilização de um estímulo naturalístico em estudos de segmentação de memória que utilizam medições electrofisiológicas.

Este estudo abre portas para investigações futuras em que será essencial determinar como ocorre a distribuição espacial deste padrão neuronal, aqui apenas sugerida devido à baixa resolução espacial do EEG, e validar a existência deste padrão em estudos cada vez mais naturalísticos, com recurso por exemplo a medições por electrocorticografia (ECoG).

Palavras-chave: Eletroencefalograma, cérebro, memória, segmentação em eventos, fronteira.

Contents

List of Figures

List of Abbreviations

ECoG	**E**lectro**co**rtico**g**ragphy
EEG	**E**lectro**e**ncephalo**g**raphy
ERP	**E**vent **R**elated **P**otential
EST	**E**vent **S**egmentation **T**heory
fMRI	**f**unctional **M**agnetic **R**esonance **I**maging
HMM	**H**idden **M**arkov **M**odels
ICA	**I**ndependent **C**omponent **A**nalysis
LORETA	**L**ow **R**esolution **T**omography **E**stimates
mPFC	**m**edial **P**re**F**rontal **C**ortex
MTL	**M**edial **T**emporal **l**obe
SLIMM	**S**chema-**l**inked **I**nteractions between **M**edial prefrontal and **M**edial temporal regions
STPS	**S**patio**t**emporal **P**attern **S**imilarity analysis
TRW	**T**emporal **R**receptive **W**indows

1 Introduction

Memories can be defined as lasting representations of previous life events that are reflected in thoughts, experiences or behaviors. They influence how other memories are formed or retrieved and shape our actions even when we are not conscious that they do so. Consciously or not, memory is influenced by the past, it is needed to carry our present daily affairs and is extremely important to plan our future.

However, memory is significantly affected by numerous neurological – Alzheimer's disease, dementia, epilepsy, traumatic brain injury, etc. – and psychiatric – schizophrenia, depression, post-traumatic disorder, etc. – conditions, and the consequences can be debilitating. For this reason, it is of extreme importance to make an effort to understand the functional organization of memory processes and their neural substrates. By making use of imaging techniques and novel approaches, neuroscientists have been working to get closer to that main goal and have, until the current day, acquired important basic knowledge which will be briefly overviewed in this first chapter.

1.1 Anatomical and Functional overview

Memory storage is believed to involve very widespread synaptic alterations in many parts of the cortex. Temporary cell assemblies are thought to maintain immediate memories, while long-term memories require more lasting strengthening of synaptic connections between the different regions of the cortex. These functional connections are then extremely important for the formation, storage and reinstatement of memories.

The most studied brain structures related to memory processes are the neocortex – the visible outer brain – and the medial temporal lobe (MTL), which contain the two hippocampi and their surrounding tissues, Figure 1.1. The neocortex, especially the prefrontal cortex, and the MTL are in constant dialogue with each other, as we store and retrieve the flow of our daily experiences.

Damage to the MTL or the prefrontal cortex commonly impairs memory in humans and animals [2]–[4]. Perhaps because these regions are anatomically remote from one another, their roles in memory have largely been considered independent, with little investigation on how they might interact to support remembering. However, efforts are now being made to understand how these two regions interact [5]. Some studies even propose that this interaction might be particularly central to the retrieval of stored information [6].

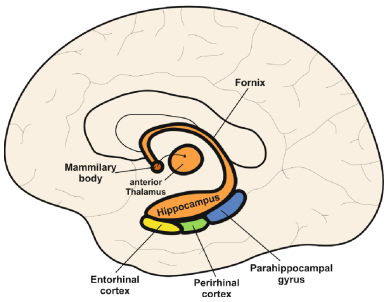

FIGURE 1.1: A schematic sagittal view of the human brain, with a focus on the MTL and associated structures. Taken from [1].

Computational network models of the MTL have attempted to examine many of the issues surrounding the functional roles of this region, predominantly focusing on the hippocampal formation and its role in memory. D. Marr [7] was the first to ascribe mathematical operations to regions in the MTL, suggesting that the hippocampal formation classifies and indexes incoming information rapidly storing it for later transfer to neocortical regions where it is reorganized during sleep. Recent computational models, that make use of machine learning approaches, have also been providing a powerful framework for understanding the distinct roles that the hippocampus and cortex play in representing memories [8]. The anatomy and function of the MTL system and its relation to the neocortex is therefore becoming well understood and computational modeling is providing a fruitful way to make these ideas more formal and quantitative.

The MTL system is now known to be fast and having limited capacity to perform a crucial function at the time of learning and establish long-term declarative memory. After learning, its role continues during a lengthy period of reorganization and consolidation whereby memories stored in neocortex eventually become independent of the MTL system. The hippocampus is ideally situated to combine information about the cognitive (neocortex) and emotional (limbic) areas, and bind that information into a memory trace that codes all aspects of consciously experienced events whereas the prefrontal cortex contributes to the performance of implicit learning and memory. This contribution appears every time that it requires search, sequencing, organization, and deliberate monitoring and it's linked to working memory.

1.2 Memory Systems

Memory takes many different shapes depending on the information being stored and for how long it is retained. The two major categories are short-term and long-term memory, based on the amount of time the memory is stored. There is also a third less discussed category called sensory memory which is the shortest-term element of memory. This type focuses on retaining sensory information after the original stimuli has ended. The ability to look at something and remember what it looked like with just a second of observation is an example of this type of memory.

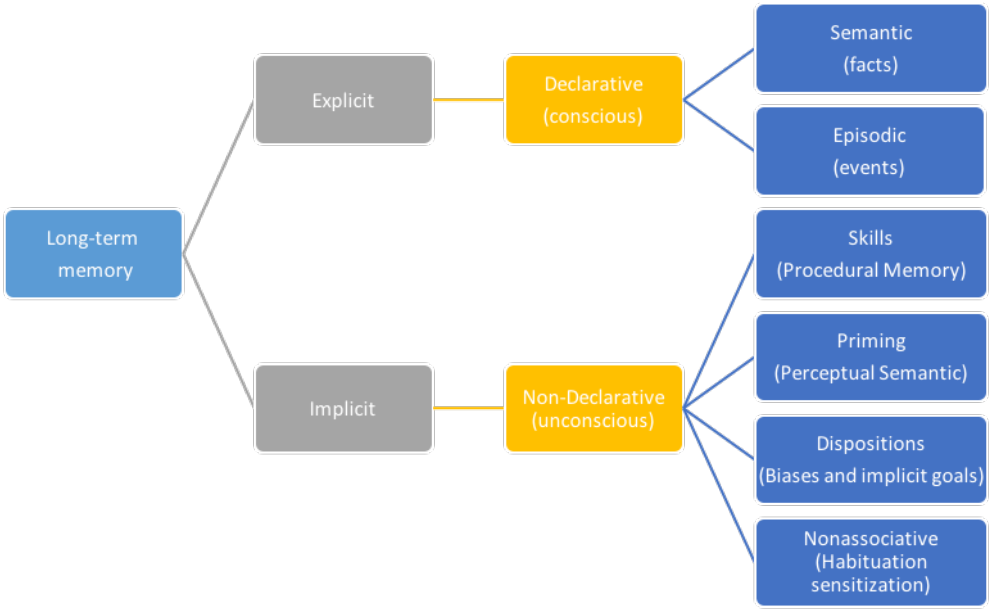

FIGURE 1.2: Classification of memory types. Declarative memories are believed to be explicit (conscious) and refer to a recollection of facts and events. Non-declarative memory, said to be unconscious, refer to a collection of abilities.

Short-term memory is responsible for storing information temporarily and determining if it will be dismissed or transferred to long-term memory, a process that takes less than a minute to be complete. This type of memory is often used interchangeably with the term *working memory*, although technically the second one refers to the whole theoretical framework of structures and processes used for the temporary storage and manipulation of information of which short term memory is just one component.

Long-term memory is the final stage of the multi-store memory model and it can be described has anything that someone remembers that happened more than a few minutes ago. These memories can last from a few days to many years, have different strengths and merge with other memories. Over the years, several different types of long-term memories have been distinguished, Figure 1.2, although their exact relationship is still a matter of debate.

The separation between declarative and non-declarative memories has been made evident by the study of patients with different brain lesions [9]. Perhaps the most famous study is that of a patient known as 'H.M', who developed a profound amnesia after having parts of his MTL, hippocampus and amygdala removed in an attempt to cure his epilepsy [2]. His ability to recall memories from well before his surgery, but his inability to create new long-term memories suggest that encoding and retrieval of long-term memories are mediated by distinct systems within the MTL, [10]. The fact that he was able to learn hand-eye coordination skills such as mirror drawing, despite having absolutely no memory of having learned and practiced the task before, suggested the existence of different types of long-term memory. Implicit memory is not accompanied by conscious awareness that one has a memory and we can only infer its existence

from the effects it has on behavior. These memories may be retrieved without an intention to remember. Some of the most studied categories of implicit memories are Procedural Memory and Priming. The first one enables us to carry out commonly learned tasks, for example riding a bike or tying a shoe, without consciously thinking about them. The second one, priming, refers to the effect of a stimulus in creating readiness for a similar one. For example, showing a picture of a face will increase the processing efficiency of a following face.

Explicit or declarative memory is memory of facts and events. It refers to memories that can consciously be recalled and can be divided into two subtypes, episodic and semantic. Episodic memory refers to memories that have specific source in time, space, and life circumstances and are often autobiographical in nature, in the way that we can travel mentally back in time to relive the experience. Contrariwise, semantic memories involve facts about the world, about ourselves, and about other knowledge that we share with a community. They are independent of the spatial and temporal context in which they were acquired and are less susceptible to forgetting than specific episodes. Initially memories are episodic, context-dependent and stored by the hippocampal complex. Over-time, they can be transformed into semantic memories in the neocortex.

A complete conception of human memory requires then multiple brain regions: the MTL for episodic memories, the prefrontal cortex for maintenance and usage of memory and sensory regions for perceptual and sensory memories. Lately research has also been indicating that the processing and storage of memory is not only sensitive to this spatial integration but also to the temporal properties of the stimuli itself.

1.3 Event Segmentation and Hierarchical Memory Processing

In our daily-life experience we are faced with a continuous stream of perceptual stimuli which arrives on a wide range of timescales, for example, one must not only identify each of the three to six syllables spoken per second but also understand their meaning as a sequence of words so that each word can achieve full meaning in the context of a sentence, and each sentence in the context of a conversation. Thus, the importance of the neural mechanisms by which information can be accumulated over time as been increasingly gaining interest on the neuroscience field. It is an intuitive fact that human observers know about the parts of everyday activities, use this information extensively in cognition and can intentionally segment the ongoing activity into different segments. Not only we segment the information we perceive but we also remember things as episodes that represent previous experiences. However, the fact that we are able to segment activity by no means reveal how we do it. What capacities does this ability enable? Is the human perceptual system sensitive to temporal segmentation during normal perception? How does the brain accomplishes it? In this chapter I will briefly overview the studies that have been trying to reach answers to these questions.

Jeffrey M. Zacks and his colleagues [11], in 2001, gave a formal definition of an event as being "a segment of time at a given location that is perceived by an observer to have a beginning and an end". Although useful, this description doesn't capture the complexity of the event conception. Events are goal-directed human representations of states of the world, with modest duration that can range from seconds to tens of minutes. They allow an organism to anticipate the future and to plan appropriate actions rather than merely react to incoming stimuli. A few years later, in 2007, the same first author [12] proposed the *Event Segmentation Theory* (EST) in which perceptual processing is guided by a set of representations called *event models* that are working memory representations, which are implemented by transient changes in neural activation. Event models are multimodal, *i.e.*, they integrate information from different sensory modalities and receive information from semantic memory representations capturing shared features of previously encountered events. By an error-based updating mechanism, event models are updated close to event boundaries in response to transient increases in prediction error. This means that, according to the EST, working memory representations are updated selectively at points in time that correspond to perceptual event boundaries. The way the updates are made is still, however, unknown. Nevertheless, Anna Schapiro *et al.* (2013) [13] presented evidence for a cluster of communities of mutually predicting stimuli, that might explain the event transitions. Through parsing behavioral, functional magnetic resonance imaging (fMRI) adaptation and multivoxel pattern analysis, they demonstrated the emergence of event representations clusters where all the events shared common temporal associations. In graphic representations of transition dynamics, groups of items with shared contextual associations become clusters or communities, Figure 1.3. When asked to mark event boundaries, after a task of selecting a number of fractals with the goal to reach a certain fractal, participants segmented sequences at points corresponding to transitions between graph communities, *i.e.*, transitions between communities with different features, despite being unaware of the temporal structures of the task.

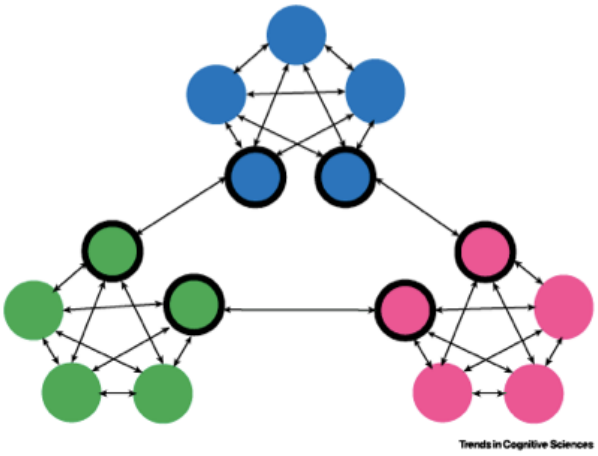

FIGURE 1.3: Community Structure described in [13]. Each community corresponds to a possible state and each edge is associated with a possible transition between states. Taken from [14].

We can interpret these discoveries in light of the EST in a way that, in the case of an event, predictions have worse accuracy at the boundaries due to a number of features (*e.g.* new movements, spatial location, characters, objects, causes, goals, or temporal separation) that change on those instances spiking a model update. Because of that, the perceptual information at those time instances receive more extensive processing in a way that results in better long-term memory. The segmentation mechanism plays then an important role on structuring memory encoding. Observers tend to agree in where they place event boundaries, and the better an individual's segmentation matches that of the group, the better they remember the events [15].

Recently, interest has turned to identifying and characterizing the neural dynamics of event representations themselves. One approach has focused on the temporal scale of event segmentation. Behavioral studies have shown that subjects can segment events into a nested hierarchy from coarse to fine timescales (that is, segment in large and small units, respectively) resulting in a segmentation that is reliable and systematically related to objective features of the stimuli, and predictive of later memory [16]. Neuronal imaging evidence of this nested hierarchy was also found in a study where fMRI was used to measure local brain activity while participants watched video depictions of everyday activities and had to press a button to mark event boundaries at a coarse and fine temporal grain [11]. In light with these findings, the EST stated that people do not perceive event boundaries on only one timescale. Rather, they perceive event boundaries on multiple timescales simultaneously, but selectively attend to one timescale choosing to attend to finer or coarser grains.

Years later on 2008, Hasson and his colleagues, using a creative movie-scrambling manipulation, characterized the duration over which representations in various parts of the cortex were sensitive to prior context [17]. They discovered a hierarchy of temporal receptive windows (TRW) which are the lengths of time before a response during which sensory information may affect that response. Early sensory areas appeared to maintain information only for short durations (short TRWs), enabling rapid processing of the ever changing sensory input, whereas higher level areas, such as the parietal and frontal cortex, maintained information for much longer time (longer TRWs) allowing them to process information from perceptual and cognitive events that unfold over time, Figure 1.4. A similar TRW hierarchy was found on the auditory and language areas by asking subjects to listen to a real life story scrambled at the time scales of words, sentences, and paragraphs [18].

In 2012 Honey *et al.* hypothesized that regions with longer TRWs would have distinctive properties in their population dynamics, more precisely slow cortical dynamics, which may be important for their capacity to accumulate information over longer timescales [20]. By applying a similar experimental approach (movie scrambling) while using electrocorticographic (ECoG) recordings they were able to focus on fluctuations of power within the broad high-frequency range of 64-200Hz, which composes the dominant portion of the variance in neural activity, and conclude that regions with longer TRWs exhibit slower ($< 0.1Hz$) fluctuations of high frequency power for both intact and scrambled movie clips. These slow fluctuations were more reliable for

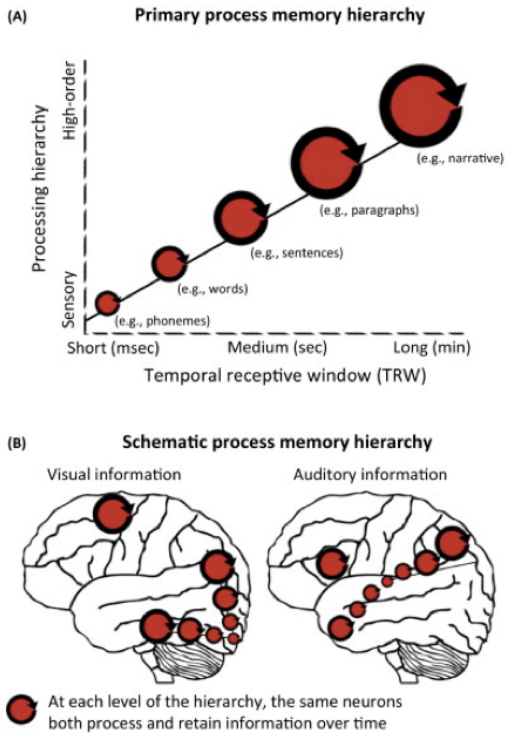

FIGURE 1.4: (A) An hierarchy of process memory in which in each region the temporal receptive windows (TRWs) increase in a topographically organized manner, from milliseconds in sensory areas up to minutes in high order regions. (B) A schematic process memory hierarchy for auditory and visual stimulation. Adapted from [19].

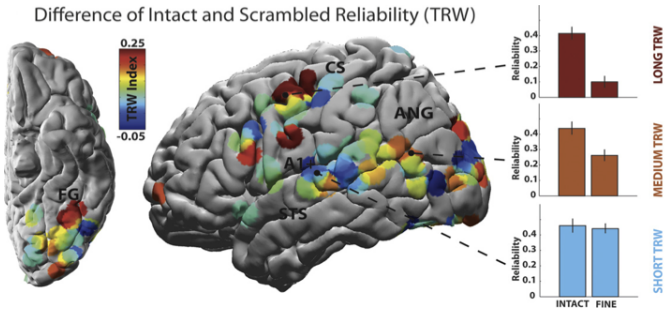

FIGURE 1.5: Reliability difference between intact and scrambled movies. Shorter TRWs are predominantly found closer to primary sensory areas, while longer TRWs further away from these areas. The TRW index is defined as the difference in response reliability between the intact and scrambled stimuli. Adapted from [20].

the intact than for the scrambled movie, suggesting that they may be connecting the processing of information over longer timescales, Figure 1.5. On the next year, similar observations across the whole cortex using fMRI recordings were made [21].

These results suggest that, not only information is processed in different timescales, but that also the dynamic timescale in each region is determined, in part by circuit properties. The responses to environmental changes in sensory areas are then optimized in a way that also makes possible to maintain and accumulate information over time in higher order areas.

After the above studies it was clear that event perception occurs differently throughout the cortex and that these different regions are indeed sensitive to the temporal organization of the stimuli itself. However, the role that this temporal organization plays on long-term memory encoding wasn't yet clear and a theory of how this process takes place as only recently been established. The *Theory of Event Segmentation and Memory* [22], Figure 1.6, states that during perception, each brain region along the processing hierarchy segments information at its preferred timescale (short events in sensory areas and longer events in high-level areas) and that chunks of information are transmitted from lower to higher levels primarily at event boundaries. In a real-life experimental approach where subjects had to watch a 50 min movie, and/or listen to the same narrated story and do a free verbal recall, they proved that all regions exhibited the hierarchical event-structured activity independently of the type of stimuli. They also proved that coarse event boundaries annotated by human observers most strongly related to long events at the top of the hierarchy while being invariant across the different stimuli (movie description of the story vs. narrative description). Most interesting, they discovered that at event boundaries in long-timescale areas, the situation model was transmitted to the hippocampus triggering it, with a peak response within several time points after the event boundary. The hippocampus could then encode the information about the just-concluded event and store these memories in a way that can be reinstated in the same long-scale cortical regions during recall. The stronger the event encoding was, the better was their reinstatement which was also related to a lower hippocampal activation during the event and a high activation at its offset. This post boundary

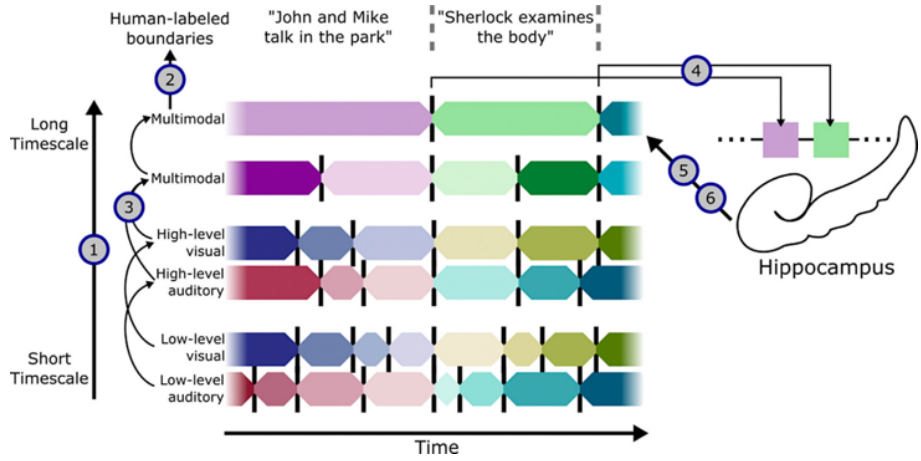

FIGURE 1.6: Theory of Event Segmentation and Memory proposed by Baldassano et. al. During perception, events are constructed at a hierarchy of timescales (1). The high-level regions have event boundaries that correspond most closely to putative boundaries identified by human observers (2) and represent abstract narrative content that can be drawn from multiple input modalities (3). At the end of a high-level event, the situation model is stored into long-term memory (4) and can be reinstated during recall back into these cortical regions (5). Prior event memories can also influence ongoing processing (6), facilitating prediction of upcoming events in related narratives. Taken from [22].

hippocampus trigger was studied in more detail by Ben-Yakov *et al.* (2018) [23] which showed that the hippocampal response, also in a movie viewing, was sensitive to boundary strength (number of participants that agreed on the boundary) and specific to cortical patterns shifts that corresponded to event boundaries. This study was based also on previous work from the same authors where they had proven that brain activity time-locked to the offset of the stimulus (event), occuring in a set of regions including the hippocampus, was correlated with subsequent memory performance [24], [25].

This boundary effect on memory performance was also shown on a study from Sols *et al.* (2017) [26] where, using pattern similarity analysis on electroencephalography (EEG), they found that when the brain detects an event boundary it triggers a rapid memory reinstatement (200-800ms from the onset of the event boundary) which might correspond to the hippocampus triggering mentioned above. The degree of neural similarity between the just encoded episode and it's boundary positively correlated with the ability to later link across different sequences of events which suggests that the better the context shifts are perceived on event boundaries, here measured has neural pattern similarities to the correspondent event, the better is the episode integration on long-term memory.

In short, the new proposed theory and later work connects the hierarchical processing framework proposed before [19] with the long-term episodic memory consolidation point of view proposed on the EST. This suggests that in segmenting our daily life continuous experiences into discrete events, the brain can integrate the information into meaningful episodic structures to

be later encoded into memory via interactions with the hippocampus. The encoded episodes are reinstated in a compressed way (*e.g.* they are summarized in the form of snap-shots separated by temporal discontinuities) [27] and in a reverse hierarchical way as they were encoded during perception, with semantic information being accessed before perceptual details [28].

1.4 Context and Motivation

Following previous work [22], [23], [26], in this project, our main goal was to uncover some of the neural mechanisms that support the event segmentation process and further explore the hypothesis that online encoding of a continuous stream of information occurs at the offset of each event, moments after a boundary is perceived.

To do so, we proposed to apply the same experimental design as used in Chen *et al.* and Baldassano *et al.* [22], [29] but on EEG data acquired from scalp in healthy participants. Although the results of those papers were promising, the temporal resolution of fMRI is severely limited by the sluggish nature of the hemodynamic response. On the other hand, EEG has a millisecond resolution, making it suitable for investigating more elementary cognitive processes.

The interest on the reproduction of this experiment also comes from two other aspects. Firstly, the realistic experimental approach itself. In real-life experience we are faced with a continuous stream of perceptual stimuli. However, memory experimental approaches are usually based on exposing subjects to a set of discrete stimuli, for example a set of photographs. Asking subjects to watch and recall a movie more closely approximates to what we currently do in our daily life when we want to remember and report something that happened in the past. Previous studies [30]–[32] have already proven that neuronal responses are indeed more reliable (reproducible) under naturalistic stimulus conditions than under conventional laboratory artificial stimuli. The second reason arises from the acquisition point of view. Since in this experimental design participants are asked to watch a 50 min movie and do a free verbal recall, this might result in a number of movement artifacts which in the case of EEG might result in unreliable data if the study design is not ideal. The data acquisition and preprocessing stages of the project were, because of this, of major importance to ensure that a good dataset was collected. Nevertheless, if the data proved to be reliable, it would validate the use of similar naturalistic stimulus in future memory related studies using electrophysiological measurements, which is something that will, without doubt, contribute for our further understanding of the dynamics of memory formation and event segmentation process.

1.5 Overview of the Thesis

This thesis reflects the work of a Master's project developed at the Branvitge Cognition and Brain Plasticity Unit of the University of Barcelona, in Spain. During my 9 months staying

at the lab, I had the chance to take part in the full life cycle of the project which involved planning the experiment, recruiting participants, acquiring data and analyzing it under the supervision and guidance of my supervisor at brainvitge, Lluis Fuentemilla, and in collaboration with Princeton University researcher, Christopher Baldassano.

Throughout the rest of this thesis I will describe the methodology applied and the obtained results. In section 2, I describe the experimental design and the acquisition equipment used to record 30 healthy participants brain signals and both the preprocessing, quantification and statistical analysis of the acquired data. In section 3, I present the obtained results divided in two sections: within events and boundary level analysis. These are followed by section 4 where I discuss the findings, its implications for the memory field and some limitations. Finally, in the last section, Section 5, I briefly summarize the results and propose future directions for event segmentation research.

2 Methods

2.1 Subject Details

Thirty three Spanish speakers (30 right-handed, 20 females, age range 18-46, mean = 22) participated for pay (10€/h). Participants were recruited from the University of Barcelona and the broader community. All participants were healthy and did not consume psychoactive substances. Informed consent was obtained from participants in accordance with procedures approved by the Ethics Committee of the University of Barcelona. Data from two subjects was discarded due to falling asleep during the experiment, and one due to the amount of noise contained in the data. Thus, the final sample of participants included in the study was thirty.

2.2 Experimental Design

Subjects were asked to watch the first 50 min of the first episode of BBC's Sherlock series, and then do a free verbal recall of the episode without cues, while being recorded using a audio recorder [22], [29]. The audio files were later analyzed in order to access subjects length and richness of the recall, with total recall times ranging from 6 min to 44 min (and a mean of 15 min). At the beginning of the movie, a 30 s audiovisual cartoon (*Let's All Go to the Lobby*) was presented to set participants attention. The experimental design was first implemented on MATLAB's latest version of Psychtoolbox [33]–[35] and then, due to some complications running the movie on the lab computer, on ePrime [36].

2.3 EEG recording and preprocessing

EEG was recorded using a 32-channel system at a sampling rate of 500 Hz, using a BrainAmp amplifier and tin electrodes mounted in an electrocap (Electro-Cap International) located at 29 standard positions (Fp1/2, Fz, F7/8, F3/4, Fc1/2 Fc5/6, Cz, C3/4, T3/4, Cp1/2, Cp5/6, Pz, P3/4, T5/6, PO1/2, O1/2) and at the left and right mastoids. An electrode placed at the lateral outer canthus of the right eye served as an online reference. EEG was re-referenced offline to the right and left mastoids. Vertical eye movements were monitored with an electrode at the infraorbital ridge of the right eye and an independent component analysis (ICA) was run

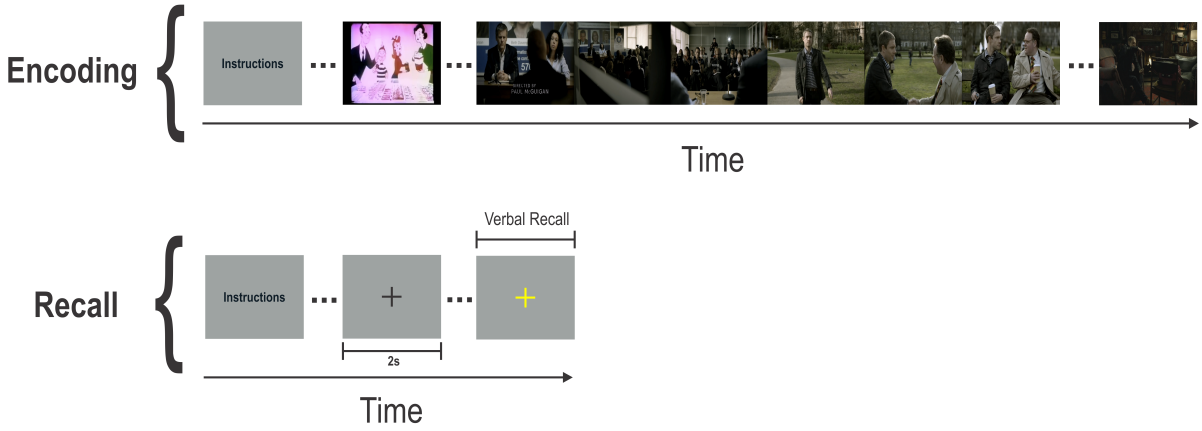

FIGURE 2.1: Experimental design similar to the one applied in [22], [29]. The participants were asked to watch the first 50 min of the first episode of BBC's Sherlock series and then do a free verbal recall of the episode.

on MATLAB's EEGlab toolbox [37] to correct for eye movements and remove extremely noisy components (no more than 6 components were removed). Using the EEGlab toolbox a low pass filter of 20Hz was applied in order to reduce the presence of muscular artifacts [38]. After that, with the aim of reducing computational time, the data corresponding to encoding (*e.g.* movie viewing) was downsampled by segmenting the EEG into bins of averaged data from one hundred sample points (*i.e.*, 200 milliseconds). We choose this interval to make sure that we were not eliminating relevant information while reducing the computational time and optimizing certain calculations. Given the nature of the stimuli, a movie, it is very unlikely to have such short meaningful information on the stimuli and so the chosen downsampling rate is valid.

2.4 Quantification and Statistical Analysis

2.4.1 Model constructed based on human annotations

We asked 6 external participants to watch the movie and write down every time they thought there was a new event, given the following instructions: "Write down the times at which you feel like there is a major change in topic, location, time, etc. Each 'event' should be more a less between 10 seconds and 3 minutes long. Don't forget to write a small description of what was happening on that specific event.". With the participants boundary annotations we looked for a statistical significant threshold, based on a permutation test (N=1000, $\alpha = 0.05$ as a cutoff for significance), and ended up selecting as boundaries the ones where more than two participants had annotated. Boundaries within three time points of one another were considered as being one. The final human annotations model was composed by 38 events which is a number in

accordance to the range found on the Chen *et al.* (2017) and Baldassano *et al.* (2017) papers [22], [29].

2.4.2 Human annotations model on neurophysiological data

After constructing the human annotations model we tested if we could find these events on the neurophysiological data. By performing a spatial-based correlation we get to assess the autocorrelation matrix along the temporal scale. To do so we started by computing spatiotemporal correlation maps, correlating the 29 electrodes with the same 29 electrodes for each of the timepoints. Next, we averaged the correlation values within each of the 38 events and ran a permutation test (N=1000) with the events shuffled in time (*e.g.* event 1 is the 10th event after one permutation and then is the 24th event after the second permutation, and so on), maintaining the length of the events. The within event correlation values were compared to the permuted values using an $\alpha = 0.05$ as a cutoff for significance.

2.4.3 Behavioral analysis

The audio files recorded during the free verbal recall were analyzed by a a lab member which was a native spanish speaker, using as a model of expected scenes the events from the human annotations model. A scene was counted as recalled if the participant described any part of the scene and counted as out of order if it was initially skipped and later described. The number of details reported in each scene was also evaluated, in a way similar to the one applied in the Levine *et al.* (2002) paper [39]. To do so the details were evaluated given the following categories:

- Event details: they are usually happenings (*e.g.*, "I fell down"), but also include who was there, reactions/emotions in others, the weather, one's clothing, physical occurrences and actions of others;
- Place details: any information that involves localization in space, including countries, bodies of water, provinces, cities, streets, buildings, rooms, and locations within a room;
- Time details: life epoch ("My twenties"), year, season, month, date, day of week, time of day, or clock time;
- Perceptual details: include auditory, olfactory, tactile/pain, taste, visual (object details, colours), spatial-temporal (allocentric-egocentric space, body position and duration).;
- Emotion/thought details: Any detail that pertains to the mental state of the subject at the time of the event. These include feeling states, thoughts, opinions, expectations, or beliefs;

- Repetitions: a detail is a repetition if it is an unsolicited repetition of a prior information-containing detail. It does not have to be a verbatim repetition, but it should not add any new information to the prior detail ("I hoped for the best. I kept my fingers crossed" - second sentence is a repetition);
- Metacomment: This category is for details that do not reflect recollection and do not fit into other categories ("Let me see if I can remember that").

The final number of details of each of the events were the sum of the details of all the categories above. This value was later normalized by dividing it by the length of time that the subject took to recall the specific event, given that usually the more details one reports the longer it takes to report that particular event. We tested if the number of details, the temporal order of recollection and the temporal length of each event were correlated with memory accuracy by performing linear regression analyzes. We also tested if the events being forgotten or not could be predicted by the autocorrelation values within each of the events using point biserial correlations.

2.4.4 Similarity within and across participants

We know from previous work that viewing the same movie or listening to the same story, e.g. facing the same stimuli, elicits similar neural responses across participants, in certain brain regions [29], [40], [41]. To assess if the neural activity patterns were similar across and within participants, given that in our experiment participants were also facing the same stimuli, we performed pairwise correlations, in a similar manner as it was applied in Chen *et al.* (2017) [29]. We started by dividing the data from the movie and from the recall part into the different events of the human annotations model, for each of the participants, and averaging the data within each of the events, resulting in movie patterns and recollection patterns for each of the events. To do this, and given that the recall data has different lengths across participants and they are smaller than the movie, the data was interpolated to the same length as the movie. We then compared the patterns between Movie and Recall, for each of the participants, by computing Pearson correlations for each of the events which results in a within participant similarity analysis, Figure 2.2A. We also computed Movie-Movie and Recall-Recall correlations by comparing the movie/recollection pattern of each scene with the movie/recollection pattern for the same scene averaged across the remaining participants. This resulted in the across participants similarity analysis, Figure 2.2B.

To assess if the correlation values were statistically significant a permutation test (N=1000) was computed, using an $\alpha = 0.05$ as a cutoff for significance, correlating the shuffled movie patterns with the recollection patterns for the Movie-Recall analysis, and the shuffled patterns of the average of the not left out participants with the left out participant patterns for both the Movie-Movie and the Recall-Recall analysis.

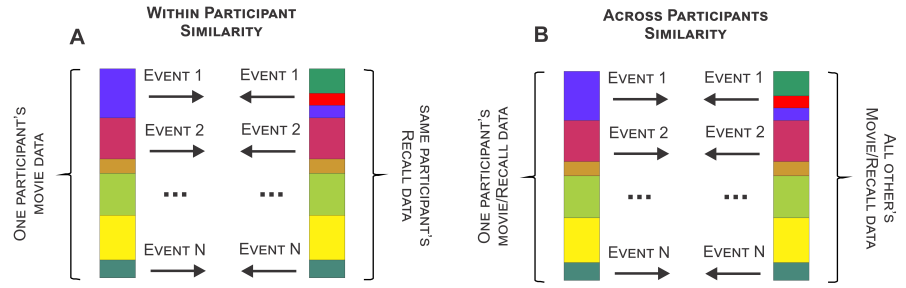

FIGURE 2.2: (A) Within participant similarity analysis schematic representation. The averaged movie patterns of each event were correlated with the same event from the recall data, for each participant. (B) Across participants similarity analysis schematic representation. The averaged movie/recall patterns of each event from one participant were correlated with the same event from the movie/recall data of the average of all other participants, repeating it for all left out participants.

2.4.5 Event Segmentation Model

To address the subjectiveness of the participants recall data, this project made use of the same data-driven event segmentation model as used on the Baldassano *et al.* (2017) [22] study to automatically segment brain activity into different events. Therefore, I will briefly explain what are Hidden Markov Models (HMM), how the algorithms behind the model work and what modifications have to be conducted so that the model can be applied to this project.

Hidden Markov Models

Only recently have HMM started to be used in the field of human neuroscience. However, the few papers already published have proved the value that this type of statistical model might have to the field. For example, Anderson, Lee and Fincham [42] used an HMM-based model to uncover temporal structures in brain activity responses during mathematical problem solving. On the same year, using an HMM to infer a number of discrete brain states, Baker and some colleagues [43] identified on magnetoencephalography recordings, transient (100-200ms) brain states with spatial topographies similar to well-known resting state networks. In 2016, Rukat *et al.* [44] proved that HMM can be used to study the dynamics of functional brain networks, by comparing this method to the classical EEG microstates analysis. This year, Baldassano and colleagues [22] proved that a data-driven HMM can be used to detect stable and abstract event boundaries in high-order areas without relying on human annotations and to reveal the event segmentation hierarchy over different regions of the cortex.

A Hidden Markov Model (HMM) is a powerful example of a statistical model. In a simpler Markov Model, known as Markov Chain, the state is visible to the observer while in a HMM the state is not directly visible (it is 'hidden') but the output (*e.g.* the observation) is. Each

state will have a probability distribution over the possible outputs. Therefore, the probability of observing one specific sequence of outputs generated by the HMM will give us some information about the underlying sequence of states. An HMM is then a probabilistic sequence model: given a sequence of observations it computes a probability distribution over possible sequences of states and choose the best state sequence.

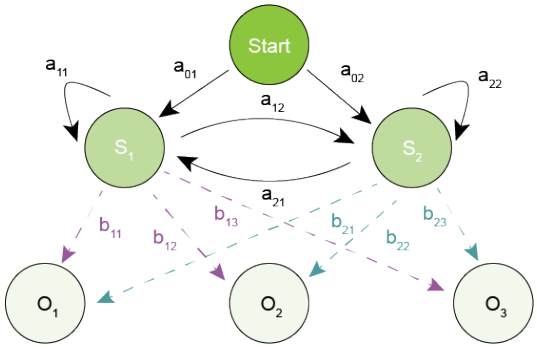

FIGURE 2.3: Example of a two state Hidden Markov Model. The black arrows represent the possible transitions between states, with the respective probabilities. In pink are represented the probabilities of having the given observations being created by state 1 and in blue by state 2.

There are three main algorithms used in HMM computations that were developed by L. E. Baum and his colleagues [45]–[47]. These algorithms are extensively described on a tutorial paper written by Rabiner [48] and will be quickly summarized next.

- The Forward Algorithm:

  The main goal of this algorithm is to compute the likelihood of a particular sequence of observations. This algorithm computes the observation probability by summing over the probabilities of all possible hidden state paths that could generate the observation sequence by implicitly folding each path into a single forward trellis. Instead of summing over all possible sequence of states, in this algorithm we sum over the probabilities of every path that could lead us to each cell of the forward algorithm trellis. Each cell, $\alpha_t(j)$, represents the probability of being in state j after seeing the first t observations. Therefore, we can compute this probability through:

$$\alpha_t(j) = \sum_{i=1}^{N} \alpha_{t-1}(i) a_{ij} b_j(o_t) \tag{2.1}$$

  where $\alpha_{t-1}(i)$ represents the previous forward path probability from the previous time step, a_{ij} represents the transition probability of changing from state q_i to state q_j and $b_j(o_t)$ represents the state observation likelihood of the observation symbol o_t given the current state. The final output will then be given by:

$$P(O|\lambda) = \sum_{i=1}^{N} \alpha_T(i) \tag{2.2}$$

- The Viterbi Algorithm:

  The Viterbi algorithm finds the single best state sequence of paths, which means maximizing $P(O|Q)$. To do so it proceeds on a similar manner as the Forward Algorithm but now each cell of the trellis, $v_t(j)$, represents the probability that the HMM is in state j after seeing the first t observations and passing through the most probable sequence of states, and can be calculated using:

$$v_t(j) = \max_{i=1} v_{t-1}(i) a_{ij} b_j(o_t) \tag{2.3}$$

  To actually retrieve the state sequence, is necessary to keep track of the path of hidden states that lead to each state and then, at the end, backtracking the best path to the beginning. To do so we take the argument that maximized (2.3):

$$backtracer_t(j) = \operatorname*{argmax}_{i=1} v_{t-1}(i) a_{ij} b_j(o_t) \tag{2.4}$$

- The Forward-backward Algorithm:

  This algorithm works by iteratively computing the best parameter estimates. First it starts with an estimate for the transition and observation probability matrices and then uses it to derive better probabilities by computing the forward and backward probabilities and dividing these probabilities among all the different paths that contributed to them. The forward probability, $\alpha_t(j)$, can be computed using the first algorithm and the backward probability, $\beta_t(j)$, (*i.e.* the probability of seeing the observations from time *t+1* to the end given that we are in state j at time t) can be computed in a similar manner:

$$\beta_t(j) = \sum_{i=1}^{N} a_{ij} b_j(o_{t+1}) \beta_{t+1}(i) \tag{2.5}$$

  The transition probability, a_{ij}, can be estimated by dividing the expected number of transitions from state i to state j by the total number of possible transitions from state i. In the case of the observation probability, b_j, the computation works by dividing the expected number of times that the model is in state j while observing a given observation by the expected number of times that the model spends on that state independently of the observation. Then it is important to define the probability of being in state i at time t and state j at time *t+1*, ξ_t, and the probability of being in state j at time t, γ_t, so that the estimated $\bar{a}_{ij}$ and $\bar{b}_j$ can be computed:

$$\bar{a}_{ij}(j) = \frac{\sum_{t=1}^{T-1} \xi_t(i,j)}{\sum_{t=1}^{T-1} \sum_{k=1}^{N} \xi_t(i,k)} \tag{2.6}$$

$$\bar{b}_j(j) = \frac{\sum_{t=1 s.t. O_{t=v_k}}^{T} \gamma_t(j)}{\sum_{t=1}^{T} \gamma_t(j)} \tag{2.7}$$

These necessary probabilities can in turn be computed based on the previous calculated forward and backward probabilities through the following equations:

$$\xi_t(i,j) = \frac{\alpha_t(i) a_{ij} b_j(o_{t-1}) \beta_{t+1}(j)}{P(O|\lambda)} \tag{2.8}$$

$$\gamma_t(j) = \frac{\alpha_t(j)\beta_t(j)}{P(O|\lambda)} \tag{2.9}$$

where $P(O|\lambda)$ can be computed using (2.2). If we iteratively use the new model $\bar{\lambda}$ in place of the previous one λ and repeat the reestimation calculation, we can improve the probability of a given sequence being observed until some limiting point is reached.

The HMM used on this project

In this project, an adaptation of the data-driven event segmentation model used in Baldassano *et al.* [22] was used. This model is a variant of an HMM in which the latent states are the events s_t and the observations are the observed brain activities b_t, Figure 2.4. From the b_t we infer both s_t and an event distinct neural signature, m_k, given by the mean brain activity pattern across a defined cluster of EEG channels. The model is set to assume that, for all the subjects, the event starts in $s_1 = 1$ and end with $s_T = K$, where T is the total number of time points and K is the total number of events that we ask the model to estimate. Given this, we assume an ergonomic model, where each time point can either advance to the next state or remain in the same one, which results in a transition matrix where all elements are zero except for the diagonal and the adjacent off-diagonal.

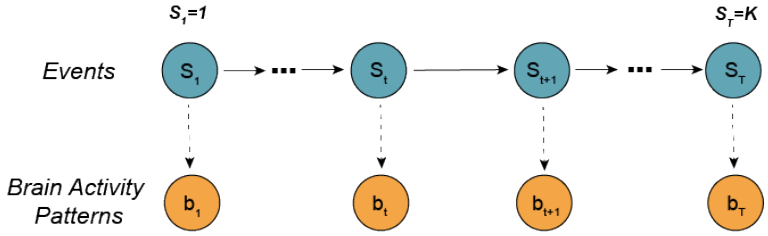

FIGURE 2.4: Hidden Markov Model implemented on the project. The events represent the hidden states which always start in $s_1 = 1$ and end in $s_T = K$ where T is the total number of time points and K the total number of events. The observations are given by brain activity patterns acquired with electroencephalography (EEG).

An isotropic Gaussian model is used to compute the observation model so that the probability that a given observation, b_t, is created by a state $s_t = k$, can be given by:

$$P(b_t|s_t = k) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-(\frac{1}{2\sigma^2})\|z(b_t - z(m_k))\|_2^2} \tag{2.10}$$

The z-scoring of the brain observations and the mean activity patterns result in a proportionality between the log probability of observing brain state b_t in an event with signature m_k and the Pearson correlation between b_t and m_k plus a constant offset:

$$log(P(b_t|s_t = k)) \propto r(b_t, m_k) \tag{2.11}$$

Given the signature estimates m_k the forward-backward algorithm is applied to compute the distributions $P(s_t = k)$ which can then be used to update the estimates for the mean activity patterns using the following expression:

$$m_k = \frac{\sum_t P(s_t = k) b_t}{\sum_t P(s_t = k)} \tag{2.12}$$

To ensure a high-likelihood solution, the observation variance, σ^2, is annealed to $4 \cdot 0.98^i$ where i is the number of loops completed by the forward-backward algorithm. When the log-likelihood starts to decrease, which indicates that the observation variance has begun to drop below the actual event activity variance, the all fitting procedure stops.

To ensure that all states are visited, the observation probabilities $P(b_t|s_t = k)$ are modified by setting $P(b_T|s_T = k) = 0$, for all $k \neq K$ so that, on the final time point, only the final state K could have generated the data. This is accomplished by modifying the backward pass to initialize $\beta(s_T = k)$ to 1 for $k = K$ and to 0 otherwise.

To ensure that all possible event segmentations have the same prior probability, a dummy absorbing state $K + 1$ is created. This insures that the transition probabilities for state K are identical to those for previous states. We set $P(b_t|s_t = K + 1) = 0$ so that this state cannot actually be used.

This model can be used on multiple datasets by running the forward-backward algorithm on each dataset and then averaging across them. It can be also used to compute how well the events estimated from one dataset fit on another one, which is accomplished by running the model on the first dataset and then using the estimated mean activity patterns and variance to compute the model for the second one.

After all the pre-processing mentioned on the previous chapter we used the mean patterns of each of the events of the human annotations model and instructed the event segmentation model to search for the same patterns on the recall data of each of the participants. Each model returns a matrix with the state estimate for each time point.

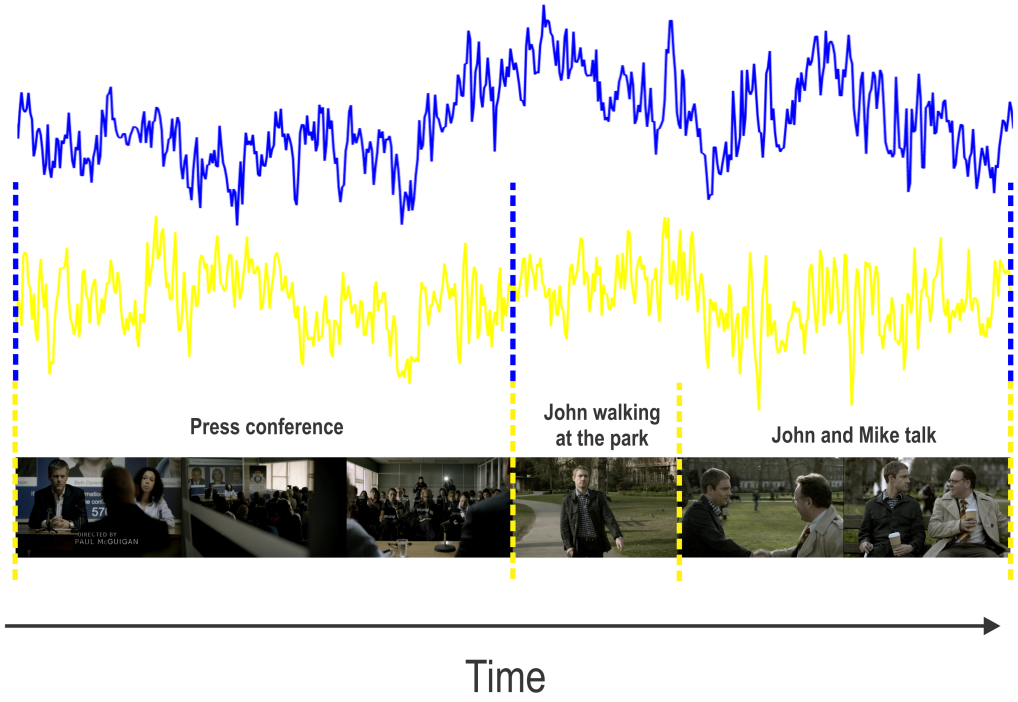

FIGURE 2.5: The data-driven event segmentation algorithm returns the most probable event segmentation model of the given brain signal. For example for the above period of the movie one signal might be segmented into three events (YELLOW) whereas another might only be segmented in two (BLUE).

2.4.6 Similarity Movie-Recall given the event segmentation model

The same comparison between the patterns of Movie and Recall for each of the participants was computed using this time the recollection patterns of the events suggested by the event segmentation model. To obtain the recollection patterns, in this case we took the learned event signatures (*i.e.* mean patterns of each of the events from the movie data) and used them to run the forward-backward algorithm on the recall data of each participant.

To assess if the correlation values were statistically significant we started by generating a null distribution based on scrumbling (N=1000) the event signatures of the movie data before running the forward-backward algorithm on the recall data. Then we computed the correlations between the movie patterns and the recollection patterns returned by the null distribution and compared them with the real correlation values using an $\alpha = 0.05$ as a cutoff for significance.

2.4.7 Spatiotemporal Patterns Similarity Analysis (STPS)

A representation similarity method was applied for calculating the spatiotemporal pattern similarity for single-trial EEG epochs [49]. The spatial features were scalp voltages from all the 29 electrodes, and the temporal features were selected using a 200 ms sliding window from the

epoched EEG data. The step size of the sliding window is one time point. Similarity was calculated using Pearson correlation coefficients, which are insensitive to the absolute amplitude and variance of the EEG response, computed between the averaged activity of the event previous to the boundary and each of the timepoints 5000 ms before and after the boundary using the above sliding windows. For each EEG epoch time bin of the boundary item, we averaged the correlation values obtained across all the 38 boundaries, thereby resulting in a matrix in which spatial and temporal information was preserved at the boundary level. A paired t-test (two tailed) was used to assess the statistical differences between the similarity patterns before and after the boundary.

To ensure that differences between before and after the boundary weren't arising just due to intrinsic temporal contiguity properties of the EEG signal, in the sense that, the further we get from a certain event the less correlated the information would be just because it happened some time in the past, we performed within, pre and post boundary, and between event correlations in sliding windows of 40 ms for 10 s before and after the boundary, for each participant. To ensure that no temporal bias was present in the analysis, within and between correlations were performed in intervals of 5 s. Within pre-boundary correlations were performed between the interval -10 s to -5 s and the interval -5 s to 0 s before the boundary. Between event correlations were performed between -5 s and 5s, were 0 corresponded to the boundary. Whereas within pos-boundary correlations were performed between the interval 0 to 5 s and the interval 5 s to 10 s after the boundary. For the spatiotemporal effect not to explain the differences between before and after the boundary the within correlations had to be higher than between so that we could see a clear boundary effect. To test this hypothesis a within measures ANOVA (3 within levels) comparing within pre-boundary, within pos-boundary and between events was computed with following post-hoc paired t-tests.

2.4.8 Event Related Potentials (ERPs)

An event-related potential (ERP) is the measured direct brain response result to a specific sensory, cognitive, or motor event [50]. To obtain the ERPs in this project, we started by filtering the data below 12 Hz so that, due to the nature of the task, we ensure that we eliminate most of the movement noise. Given that ERPs are in general neural responses time locked to an event that is consistent over trials, the very rapid neural responses tend to be eliminated when we average across trials and we end up with mostly ERP components that are relatively slow ($< 12Hz$), so the choice of filtering the data using such a low frequency doesn't affect greatly the analysis. The EEG data was then epoched around each of the boundaries of the human annotations model into 6000 ms segments (-2000 to 4000 ms relative to the boundary onset), and the pre-boundary interval (-100 to 0 ms) was used as the baseline for the baseline correction procedure. For each participant, we separated the epochs as belonging to two categories, recalled and forgotten, if the event before the respective boundary was evaluated as recalled or not during the audio files analysis. ERPs were investigated starting at 0 ms to 2000 ms after each boundary

onset. A paired t test (two tailed) was used to assess the statistical difference between the two conditions ERPs.

2.4.9 Non parametric cluster-based permutation test

To correct for multiple-comparison we employed a nonparametric statistical method based on cluster-level randomization testing to control the family-wise error rate. This method was implemented in the open source software Fieldtrip [51]. Statistics were computed for every time point, and the time points whose statistical values were larger than a threshold ($p = 0.05$, one tail) were selected and clustered into connected sets on the basis of temporal and spatial adjacency. The observed cluster-level statistics were calculated by taking the sum of the statistical values within a cluster. Then, condition labels were permuted 1000 times to simulate the null hypothesis and the maximum cluster statistics was chosen to construct a distribution of the cluster-level statistics under the null hypothesis. The nonparametric statistical test was obtained by calculating the proportion of randomized test statistics that exceeded the observed cluster-level statistics.

2.4.10 Low-resolution tomography estimates (LORETA)

Given the low spatial resolution of EEG, standardized low-resolution tomography (sLORETA) of scalp potentials was used to search for possible cortical activity differences between events that were recalled and events that were forgotten. This method performs localization inference based on images of standardized current density, which corresponds to the 3D distribution of electric neuronal activity that has maximum similarity (*i.e.* maximum synchronization), in terms of orientation and strength, between neighbouring neuronal populations (represented by adjacent voxels). It has very low spatial resolution which decreases with depth. Given so, the outputs can only be seen as speculations of possible sources. To apply it, the average of all the boundaries for the statistical significant period, for each participant, divided in recalled or forgotten considering the event previous to the respective boundary, was used as an input in the sLORETA software [52]–[54]. The difference between recalled and forgotten was computed and the neural current source distributions were evaluated for this difference.

3 Results

3.1 Human Annotations Model

Because we expected the EEG signal to pick up activity from mostly higher order areas, and since in the Baldassano *et al.* paper [22] it was proven that higher order regions tend to segment information in accordance to human annotations, we started by constructing a model based on the annotations of six external participants. The first thing we noticed when looking at the boundary annotations from the six external participants was that they were quite consistent across them, Figure 3.1, which is in agreement with the idea that when faced with the same stimuli people tend to segment the information in the same manner, especially if they have the same interpretation of the scene [22], [40], [55], [56].

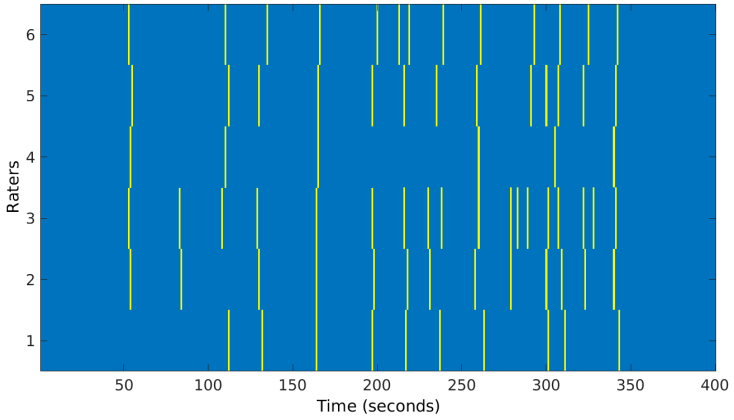

FIGURE 3.1: Boundaries identified by the six external participants, for the first 400 seconds of the movie.

After finding the best threshold we found that the best model contained 38 events, which can be seen in Figure 3.2. Each box represents a certain event and its size represents the length of that particular event. Given so, we can see that the model contains a greater number of shorter events in the beginning of the movie and a gradual increase of the length of the events which is in agreement with the movie construction where the beginning contains a number of faster transitions of features, such as spatial and goal directed features.

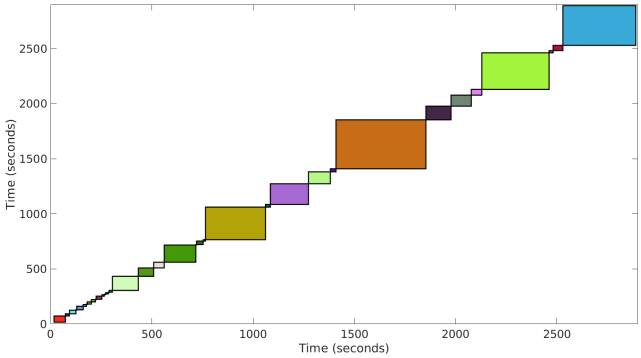

FIGURE 3.2: Model constructed based on the human annotations. We can visualize the 38 events obtained and their different lengths which is due to the fact that the scenes in the movie have different durations.

3.2 Neurophysiological data - Within events analysis

3.2.1 Encoding Data

We know, from previous papers, that events share a number of features which change on event boundaries and that it is this transition that initiates the segmentation mechanism [12], [13]. Because of this we expected that within the events the correlation would be higher than across them. So after the preprocessing of the data we started by looking at the spatiotemporal correlation maps to check if it was possible to see some kind of clustering of the signal into events. The autocorrelation maps revealed some patterns that were quite stable across participants and where some clusters seemed to exist, Figure 3.3. A small one in the beginning, one in the middle and a big one in the end which could be segmented in smaller ones when looked closer.

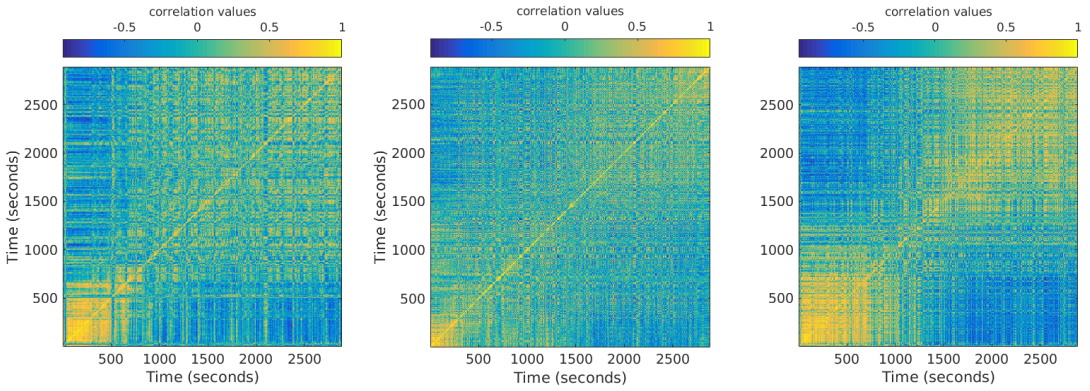

FIGURE 3.3: Spatiotemporal correlation maps for three participants. The pattern appears to be stable across participants and three major clusters of activity are visible, which can then be segmented into smaller ones with further inspection.

When plotting the model constructed with the human annotations on top of the correlation maps we saw that some of the events seemed to fit quite well to the data, Figure 3.4.

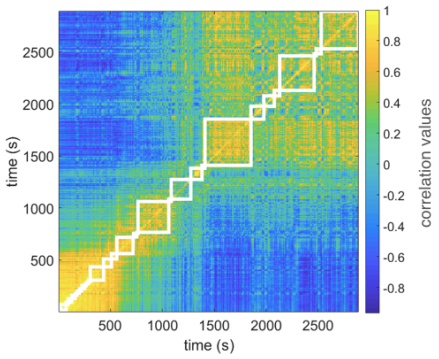

FIGURE 3.4: Spatiotemporal correlation map for one participant encoding data with the human annotations model plotted on top. The model seems to fit quite the spatiotemporal patterns and identifies some clusters that might correspond to specific events.

To assess if the data was picking up information in accordance with the human annotation model we averaged the autocorrelation values within each of the 38 events and we tested this value against a permutation test (N=1000) where the events in the model were shuffled (keeping the length of each event).

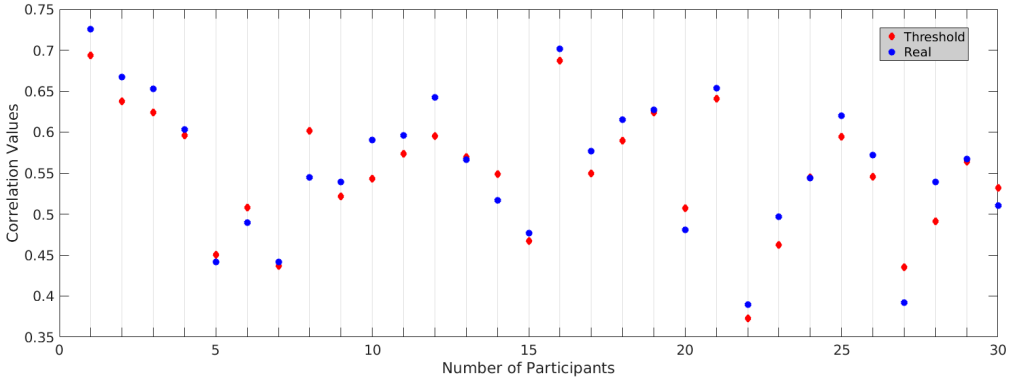

FIGURE 3.5: Within event correlation values (BLUE) and statistical threshold values (RED), obtained by performing a permutation test (N=1000), averaged across events for each participant.

After averaging the values across events for each participant we verified that for 22 participants this value was above the threshold, Figure 3.5, and it was significant at the group level ($p < 0.05$, two tail). These results show that the EEG patterns seem to reflect the temporal structure of the movie encoding which lead us to think that the neurophysiological data might contain information encoded in the manner of events that seem to be related to the human annotations.

3.2.2 Recall Data

Next we looked at the data recorded during the free verbal recall to question if this neurophysiological data was also showing some event segmentation and if the patterns were similar to encoding. To compare it to the first part we interpolated the signal so that it had the same time points as the movie. We were surprised to see that the cluster patterns were similar to the ones found on the encoding data. Again, when plotting the model constructed with the human annotations on top of the correlation maps, we saw that some of the events seemed to fit quite well to the data too, Figure 3.6, although not so well as they did to the encoding data.

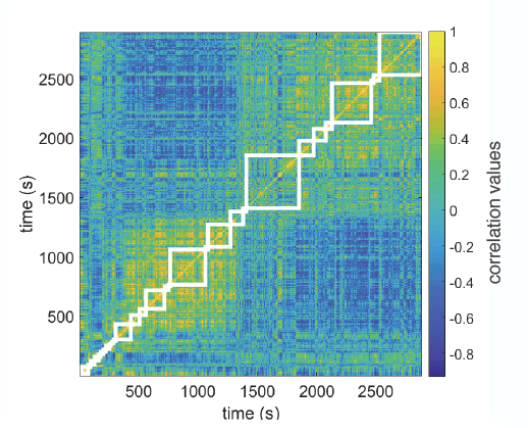

FIGURE 3.6: Spatiotemporal correlation map for one participant recall data with the human annotations model plotted on top. The model seems to fit some of the spatiotemporal patterns, althought not so well as in the movie data, and identifies some clusters that might correspond to specific events.

To assess if the events recalled were also in accordance with the human annotation model we performed the same test as before. After averaging the values across events for each participant we verified that for 14 participants this value was above the threshold, Figure 3.7, which wasn't significant at the group level ($p > 0.1$, two tail). At one tail level 18 of the participants were above the threshold. These results, although not significant, might indicate that some of the events might be recalled in the same manner as they were encoded. Since most probably a lot of events encoded during the stimuli presentation were latter forgotten it is reasonable to think that, that is why the human annotation model didn't fit so well the neurophysiological data as it did in the encoding. Also, given that participants describe differently the events, some taking longer than others, it might also justify why the events from the human annotations model didn't fit well to the recall data.

3.2.3 Recall Ratings and Behavioral Analysis

To evaluate the memory performance of the participants on the verbal recall we used the constructed model to rate the number of events that participants verbally recalled. We saw that

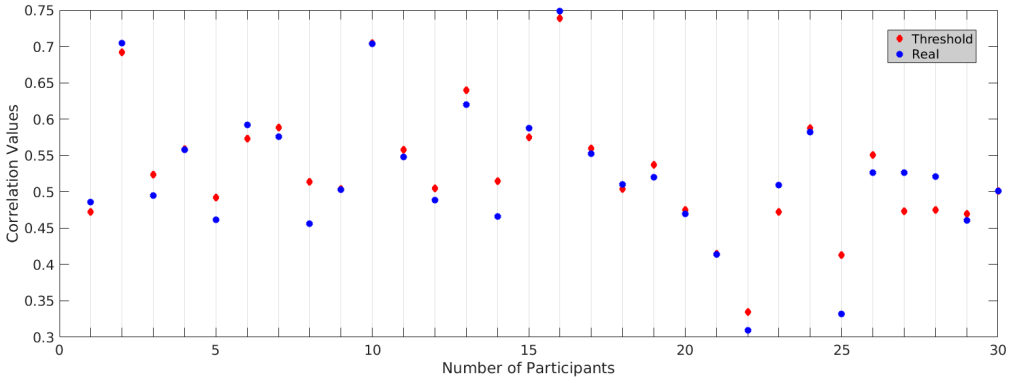

FIGURE 3.7: Within event correlation values (BLUE) and statistical threshold values (RED), obtained by performing a permutation test (N=1000), averaged across events for each participant.

17/30 participants recalled more than 50% of the events and that the pattern of recalled events shows a resemblance to the clusters in the autocorrelation matrices and a consistency across subjects, Figure 3.8.

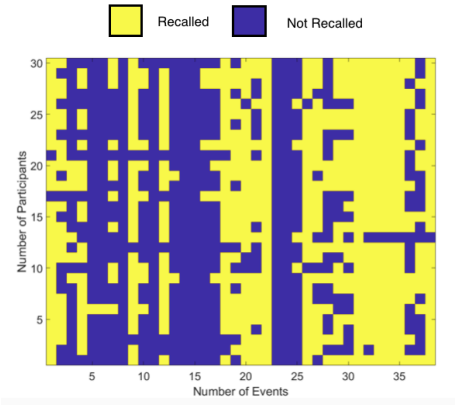

FIGURE 3.8: For each participant, the events that were recalled (in yellow) and the ones that were forgotten (in blue) are despicted.

To make sure that participants were reporting the events in the same order as they appeared in the movie, we ran a linear regression analysis. If the temporal order revealed a linear fit it would mean that they were ordering the events correctly, which was exactly what we found by comparing the regression values with zero on a t-test ($p < 0.05$, two tailed). Knowing this we wanted to see if temporal order or temporal length of the events were correlated with participants memory accuracy during the recall test. Only temporal length revealed to be correlated with accuracy, Figure 3.9, which we expected given that the longer an event was the more information contained and the easier would be to later recall part of this information.

We also investigated if the correlation values within the events could be predictive of their later recall. To do this we calculated the point biserial correlation. For most of the participants

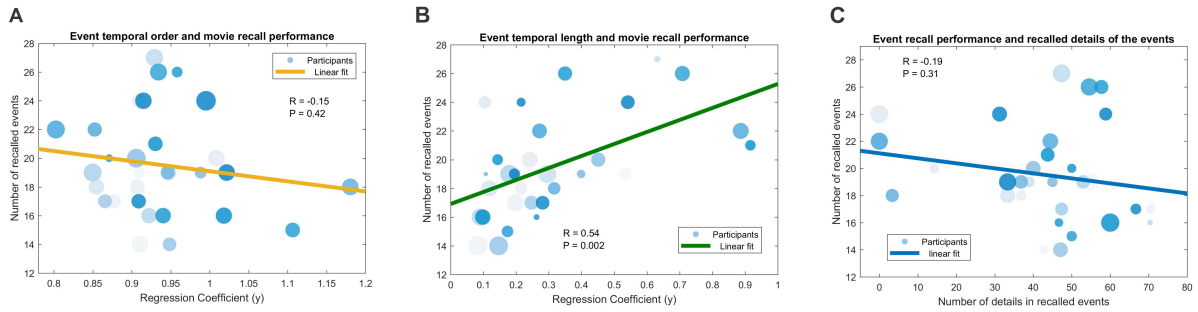

FIGURE 3.9: (A) Linear Regression Analysis for event temporal order and movie recall accuracy. (B) Linear Regression Analysis for event temporal length and movie recall accuracy. (C) Linear Regression Analysis for number of recalled details and movie recall accuracy.

we found negative correlations and p-values above chance ($p > 0.05$, two tail). This seems to indicate that the correlation values within events can't be used as a prediction of later recall.

3.2.4 Similarity within (Movie-Recall) and across (Movie-Movie; Recall-Recall) participants

To check if the patterns were similar across participants and between the movie and the recall we performed pairwise correlations, in a similar manner as it was applied in the Chen *et al.* (2017) paper [29]. We started by performing a within participant analysis where we compared the movie patterns with the recollection patterns for each of the participants, Figure 3.10.

In contrary to the Chen *et al.* (2017) paper [29] results, we didn't find any similarity between the movie and the recollection patterns within participants ($p > 0.05$, at the group level). However, this could be explained by either the fact that the recall data contains higher quantities of noise than the encoding data or by the simple fact that participants weren't recalling the events in a similar manner as the human annotations model, as we proposed before when we didn't found significant results at the group level in the within event autocorrelation analysis.

We next examined the correlations between movie patterns of each participant compared with the averaged movie patterns of the remaining participants. Given previous work where it was proven that viewing the same movie or listening to the same story, *e.g.* facing the same stimuli, elicits similar neural responses across participants, in certain brain regions [29], [40], [41], we expected to find similar neural patterns across participants. Our analysis revealed that there was in fact a high level of similarity across participants ($p < 0.05$, at the group level), Figure 3.11.

We next performed a similar across participants analysis but using the recollection patterns and, as in Chen *et al.* (2017) [29], we also found high levels of similarity between participants ($p < 0.05$ at the group level), Figure 3.12. These results suggest that across-participants similarities

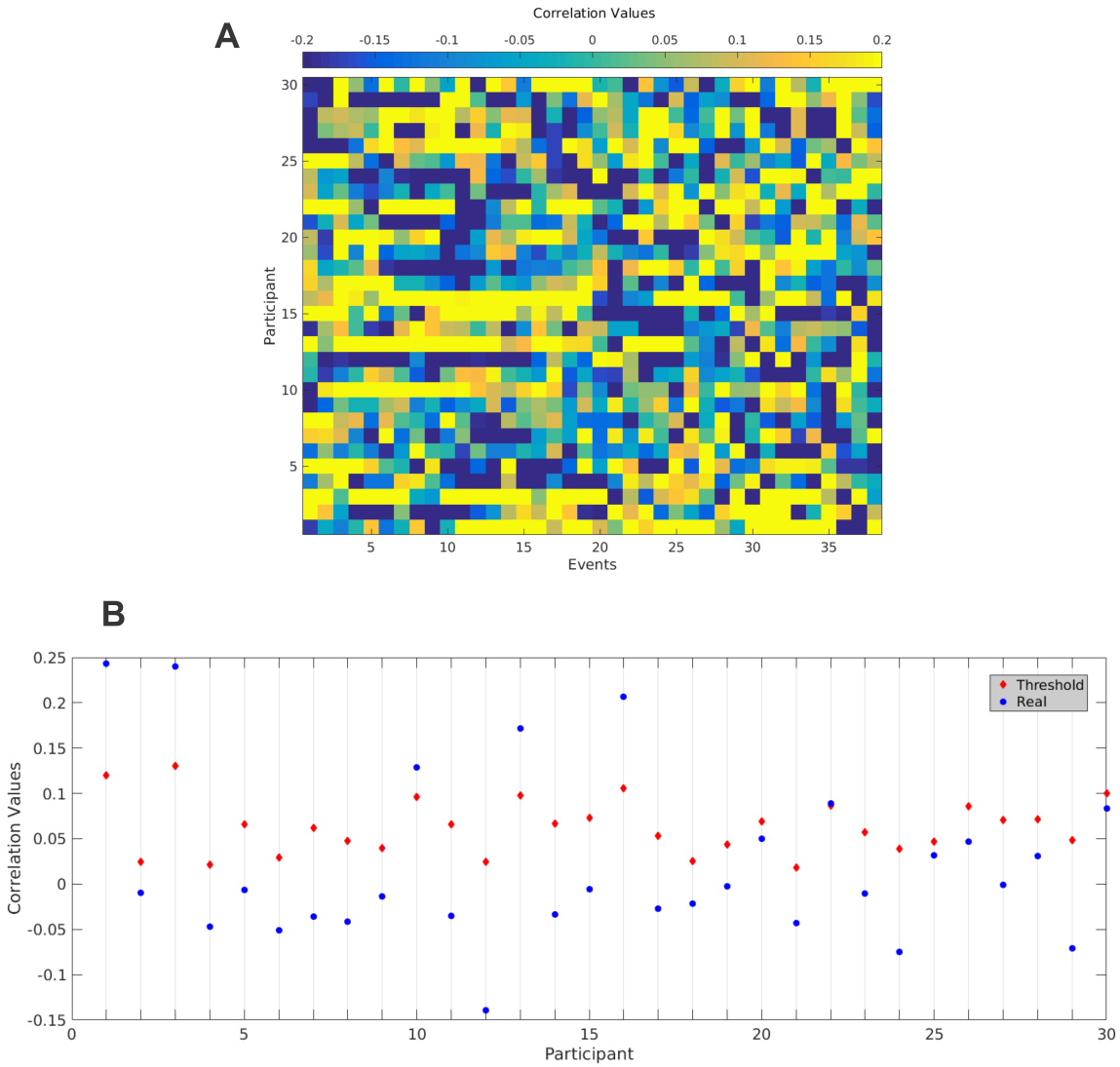

FIGURE 3.10: (A) Correlation values between movie patterns and recollection patterns, for each participant and for each event. (B) Averaged correlation values (BLUE) and statistical threshold values (RED), obtained by performing a permutation test (N=1000), for each participant.

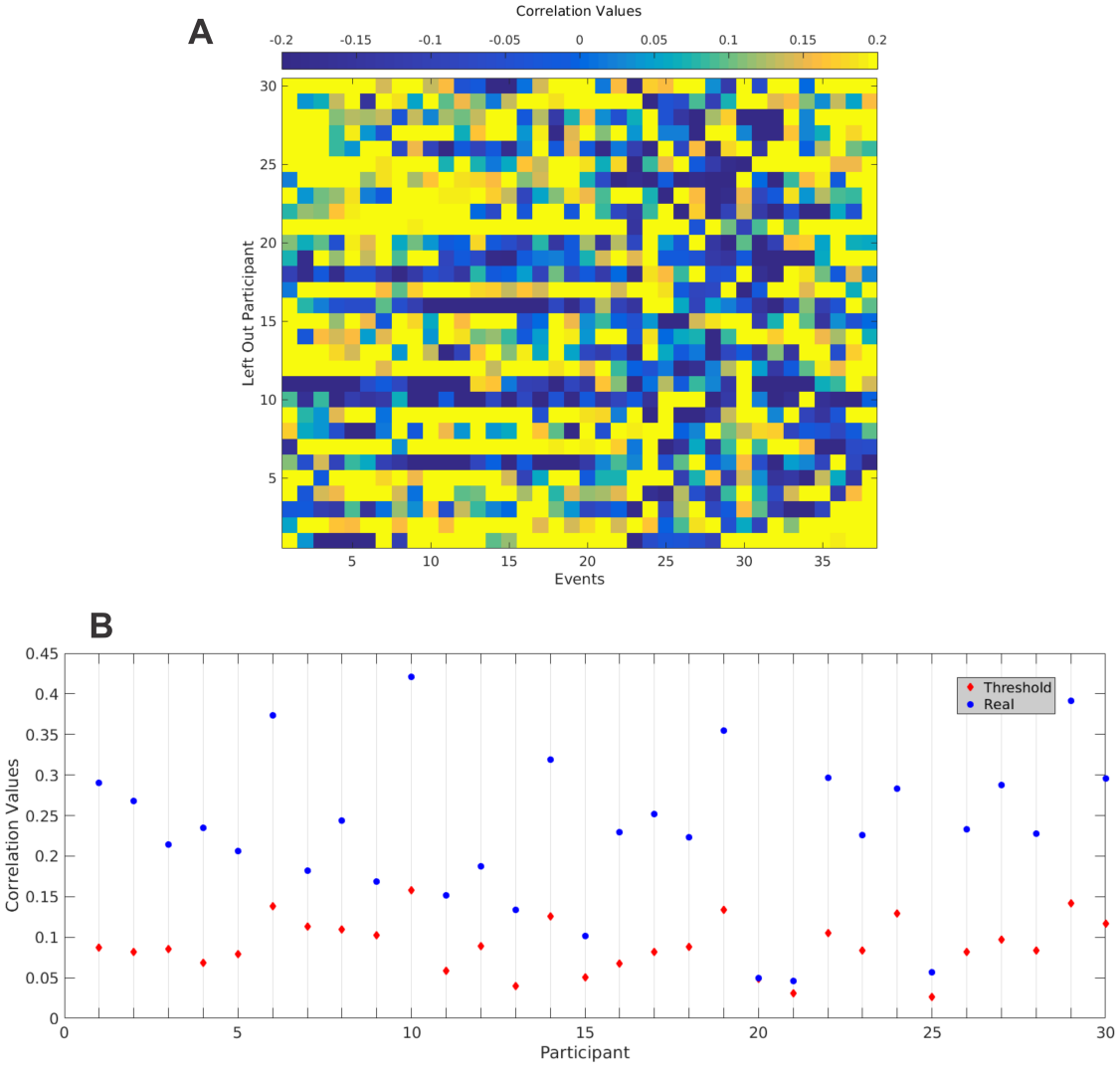

FIGURE 3.11: (A) Correlation values between movie patterns of one participant with the averaged of the remaining participants, for each left out participant and for each event. (B) Averaged correlation values (BLUE) and statistical threshold values (RED), obtained by performing a permutation test (N=1000), for each left out participant.

might also be present during recollection, even though during the recall session there was no stimulus presentation and each participant described the movie scenes in their own words and taking different durations.

The across participants analysis suggested that participants share similar neural patterns during movie viewing and later recollection. However, the within participants analysis suggested that encoding and recall didn't demonstrate similar neural activations. Besides the above stated possibilities, another would be that the human annotations model is not the best segmentation of the recall data given that participants recall the movie differently. A more subjective segmentation of this part of the data would be needed to really conclude if the neural patterns are indeed different between encoding and recall.

3.2.5 Similarity Movie-Recall with Event Segmentation Algorithm

We used the mean patterns of each of the events of the human annotations model to search for the same patterns on the recall data of each of the participants. Each model (one for each participant) returns a matrix with the state estimate for each time point.

Then, we used these models to compare the event patterns between Movie, using the events of the human annotations model, and Recall, using the outputs of the algorithm, for each of the participants using the within participants similarity analysis as used before.

Movie and Recall weren't similar when we used the events based on the human annotations model to compute the recollection patterns. However, when we used the data-driven event segmentation models we get a significant similarity between the two ($p < 0.001$, at the group level), Figure 3.13. This confirms our previous proposition that, given that participants recall the events differently and with different lengths, the human annotations model is not the best fit for the recall data. The event segmentation model is powerful enough to return the best segmentation of the 38 event for each particular participant and in doing so we were able to find similar results as the Chen *et al.* (2017) paper [29]. These results show that during verbal recall of the movie, neural patterns associated with individual scenes were reactivated in the absence of any external cues which proves that encoding and recall occur in a similar manner, *e.g.* by the form of events.

3.3 Neurophysiological data - Boundary level analysis

The above analysis focused mostly on what was happening inside the events so next, we turned our attention to what was happening at the boundary level. Previous papers suggest that encoding of information related to an event takes place moments after a boundary takes place and it is these context shifts that facilitate later memory reactivation [22]–[26]. Following these results we wanted to see if we could find evidence for a boundary effect and if any difference on

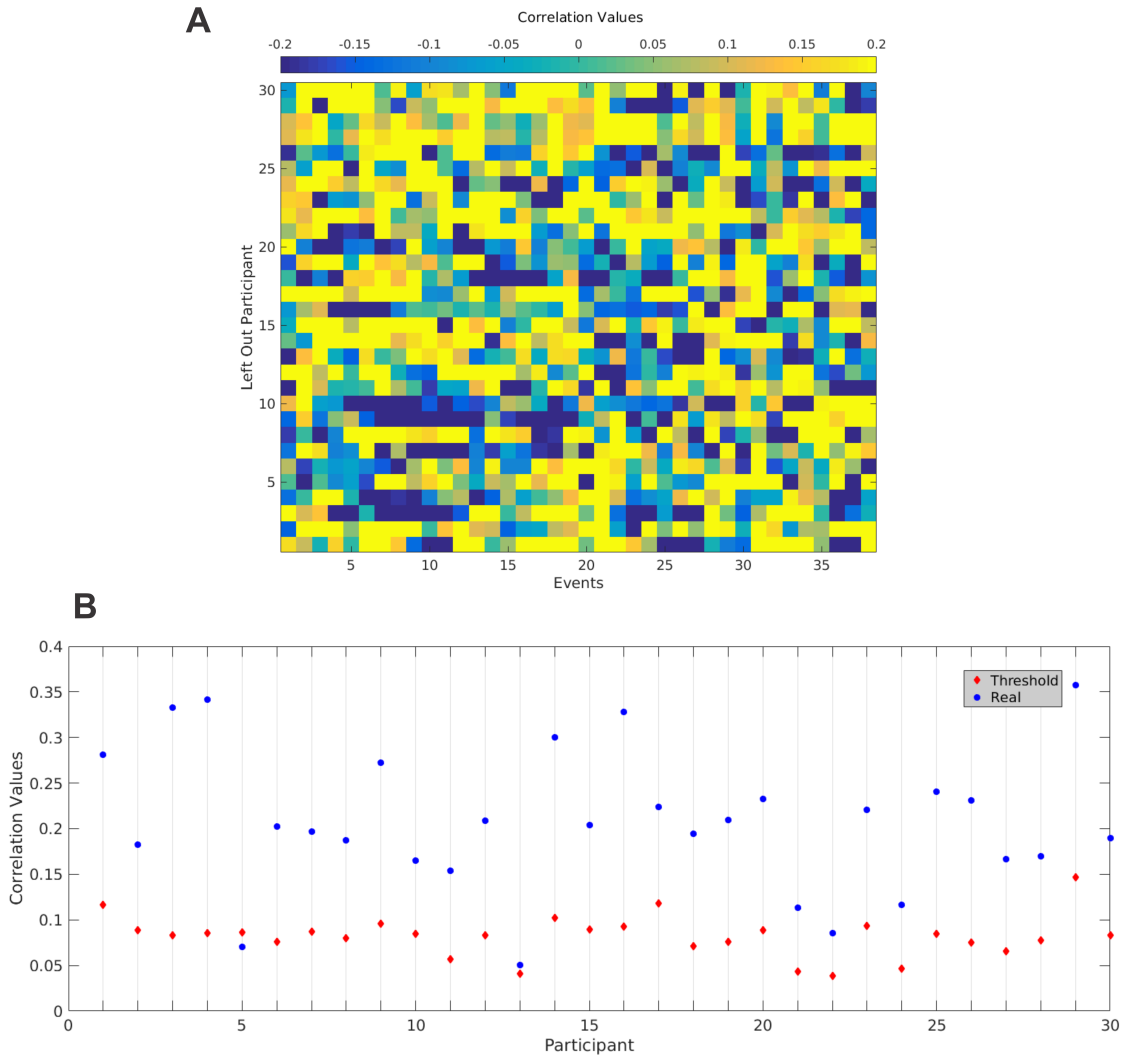

FIGURE 3.12: (A) Correlation values between recollection patterns of one participant with the averaged of the remaining participants, for each left out participant and for each event. (B) Averaged correlation values (BLUE) and statistical threshold values (RED), obtained by performing a permutation test (N=1000), for each left out participant.

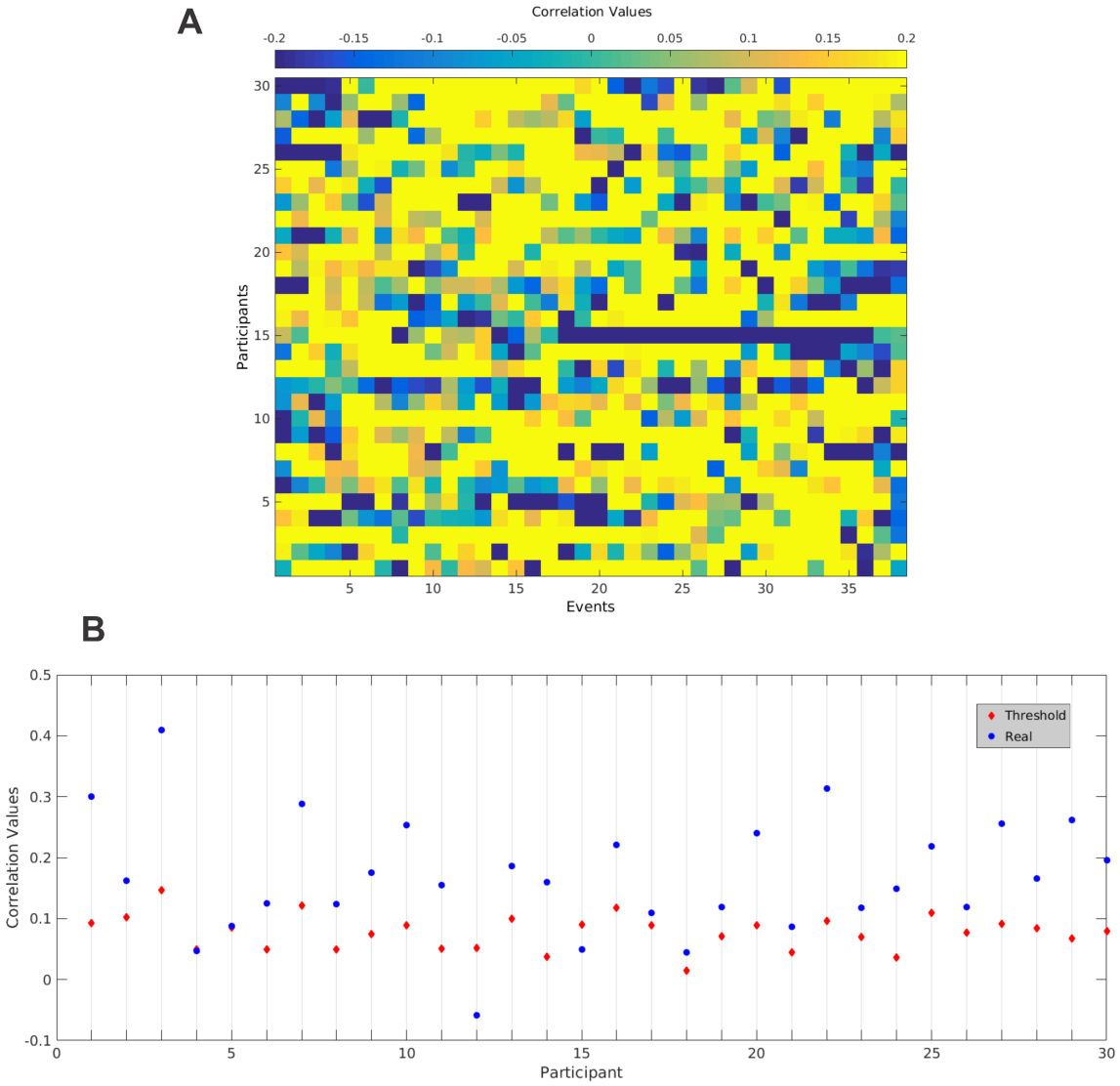

FIGURE 3.13: (A) Correlation values between movie patterns from the events of the human annotations model with the recollection patterns from the events returned by the event segmentation algorithm, for each participant and for each event. (B) Averaged correlation values (BLUE) and statistical threshold values (RED), obtained by performing a permutation test (N=1000), for each left out participant.

neural activity was present, after a boundary, that could explain an event being later recalled or forgotten.

To test the hypothesis that we are indeed looking at information that is perceived at the boundary level, a spatiotemporal pattern similarity (STPS) analysis was conducted. To do so we correlated the mean pattern activity of the just encoded event with each of the time points of the 5 s before and after the boundary, using a sliding window of 200ms to smooth slightly the data.

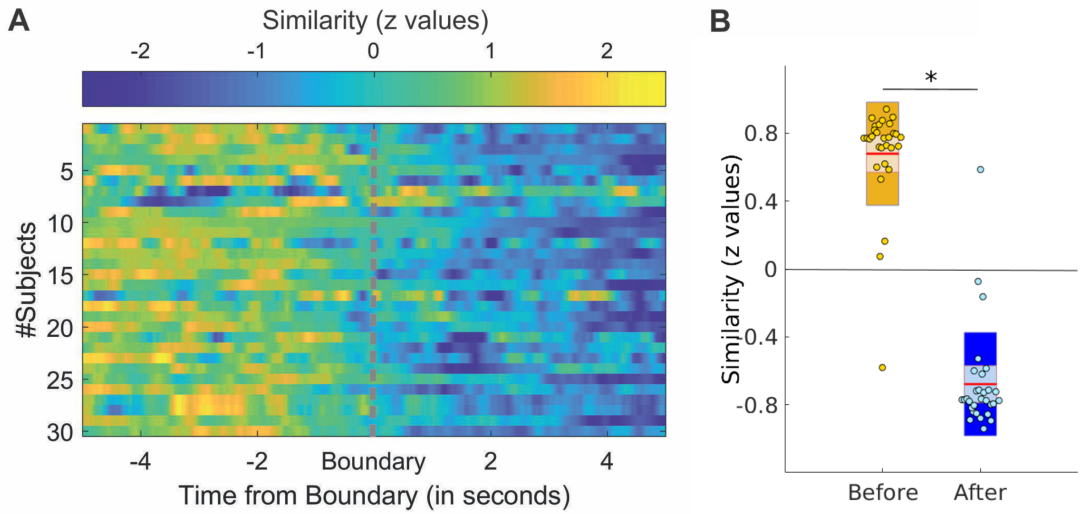

FIGURE 3.14: (A) Spatiotemporal similarity pattern correlations for 5 s before and after a boundary, for each participant. (B) Similarity values, for before and after the boundary. The asterisc indicates that there is a statistical significant difference between the two ($p < 0.05$, two tail).

The similarity patterns depict positive values before the boundary and negative after it, Figure 3.14. A t-test between the similarity values before and after the boundary was applied and returned a statistically significant difference between the two ($p < 0.05$, two tailed). However this transition to negative correlation values could be explained by the fact that the more distant the information gets and new information appears the more anti-correlated would be the neural patterns. If this was true then when computing similarity values within the event before the boundary and after the boundary the correlation patterns would show differences due to their spatiotemporal distance. To assess this we performed Pearson correlations between two intervals of 5 s within the pre-boundary event, within the pos-boundary event and between the two events.

As we can see in Figure 3.15A, within event correlations depict higher similarity values than between event patterns with a significant effect ($F(2,58)=13.94$, $p < 0.001$) revealed by a repeated measures ANOVA (3 within levels) comparing the three categories. Post-hoc paired t-test showed that within event similarity, both pre-boundary and pos-boundary, were higher than between event similarity ($t(29) = 4.44$, $p = 0.0001$ and $t(29) = 3.46$, $p = 0.001$, respectively) and that the two within similarities didn't differed between them ($t(29) = 0.83$, $p =$

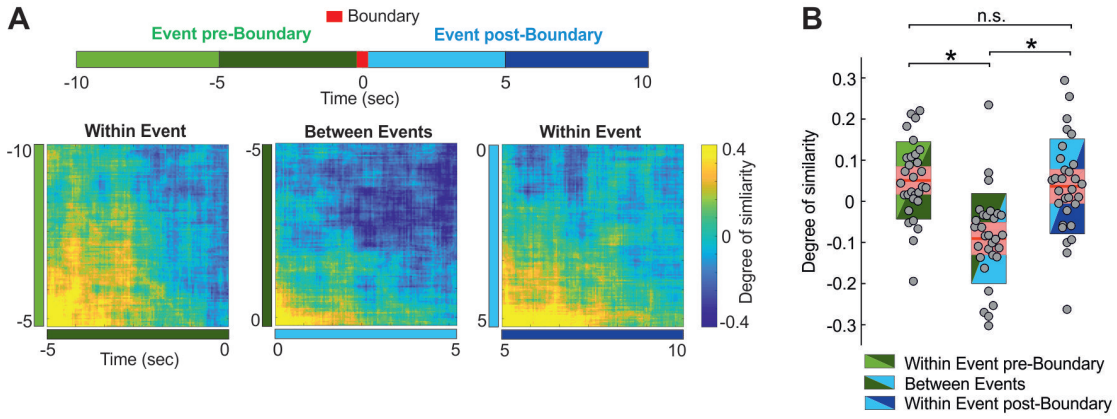

FIGURE 3.15: (A) Spatiotemporal similarity pattern correlations for the within pre-boundary event (computed by correlating the interval -10 s to -5 s with the interval -5 s to 0), between events (computed by correlating the interval -5 s to -5 s), and within pos-boundary event (computed by correlating the interval 0 to 5 s with the interval 5 s to 10 s), averaged across participants and z scored. (B) Boxplot with averaged similarity values for each participant and for each category were the asterisc represents a satistically significant difference ($p < 0.05$, two tail) and a n.s a non significant difference ($p > 0.05$, two tail).

0.41), Figure3.15B. With this results we can conclude that indeed a boundary effect occurs during encoding of a movie which results in the segmentation of the perceived information in a number of events. The difference between before and after the boundary suggest that, because many different features change between events, activity patterns within the new event are anti-correlated with the previous one. The more into the new event we get, the more negative is the correlation which indicates that our brain activity switches from encoding the previous event to perceive and encode the new arriving information.

To assess what was happening at the boundary level we computed the ERPs for each of the boundaries and for each of the participants, for all the 29 electrodes. Next we divided them into two categories, recalled or forgotten, if the event previous to the respective boundary had later been reported on the free recall or not. The average across trials and participants for four representative electrodes can be visualized in Figure 3.16.

As it can be seen in Figure 3.16, there is a clear distinction between the recalled and forgotten categories, around the period identified by the gray shade. Most surprisingly, we found evidence of the N400 component on the events that were recalled. The N400 component is a negative-going voltage occurring approximately 400 ms after the stimulus onset that has been linked to the semantic integration of a given stimulus into a previous context, *e.g.* the more incongruent the new context is the more prominent is the N400 activity [57]–[59]. The presence of this component in our case seems to indicate that when a boundary occurs, because of the incongruence between the previous and the new event, there might be an enhancement of memory consolidation of the just encoded event.

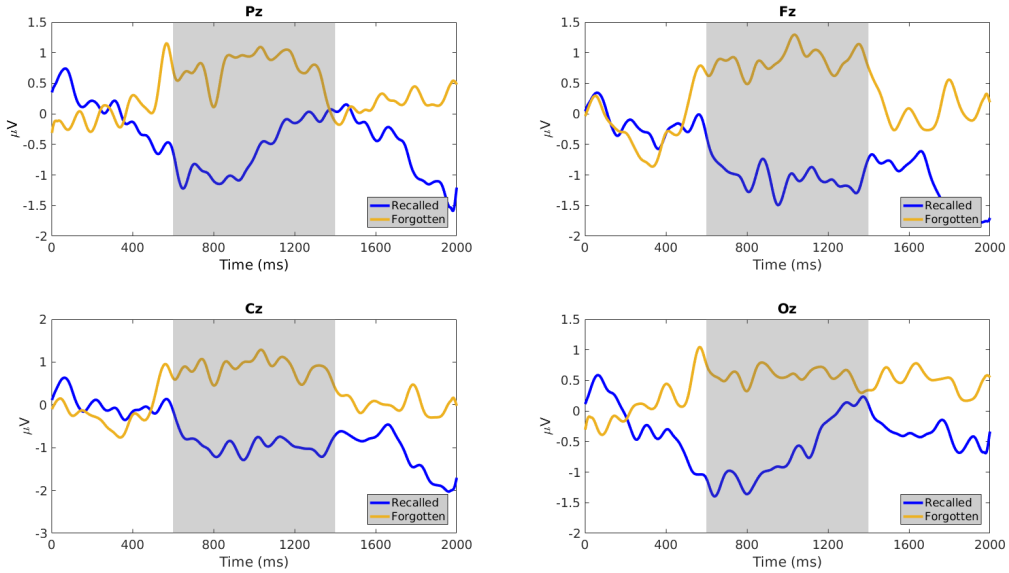

FIGURE 3.16: ERPs from four representative electrodes, obtained for 2000 ms after the boundary, and divided between recalled (BLUE) and forgotten (YELLOW) if the event before each boundary was later reported during the free verbal recall or not.

To evaluate if the difference found between recalled and forgotten was significant a t-test was performed and a cluster permutation analysis was ran which revealed a cluster of significant values ($p < 0.05$, one tail) around the period of the N400 appearance, Figure 3.17. This cluster shows a left anterior-posterior pick of activity although being mostly distributed over the scalp.

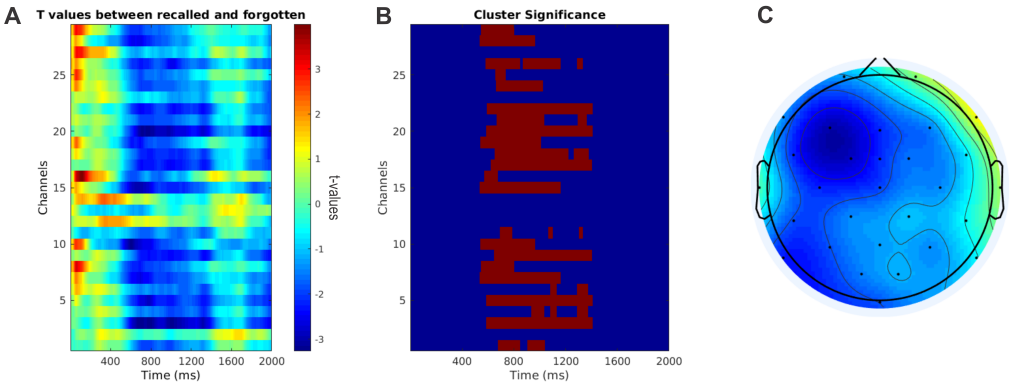

FIGURE 3.17: (A) T-values between recalled and forgotten ERPs. Negative t-values appear around the N400 period. (B) To test if these values are statistically significant a cluster permutation analysis was performed which returned a significan cluster ($p < 0.05$, one tail) for the N400 period. (C) A topoplot with the scalp activity of this cluster reveals a left fronto-occipital pick of activity.

The results until here suggest that information from the previous event is integrated into

memory moments after a boundary occurs. But what if the activity at the boundary is related instead with the new event and not the previous one? To make sure that the N400 was predicting memory storage of the previous event and not the one after the boundary we computed the ERPs considering as forgotten/recalled the new event instead of the previous one, Figure 3.18.

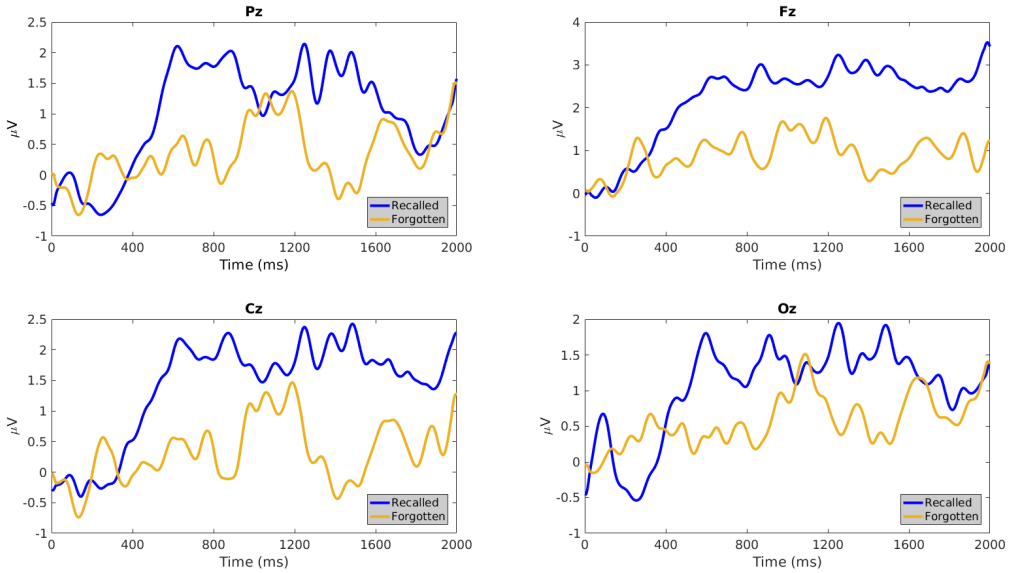

FIGURE 3.18: ERPs from four representative electrodes, obtained for 2000 ms after the boundary, and divided between recalled (BLUE) and forgotten (YELLOW) if the event after each boundary was later reported during the free verbal recall or not.

This time no statistical significance was found between recalled and forgotten, confirming that the activity after the boundary is related with memory of the previous event and not the new one.

We also computed contingency tables, like the one in Figure 3.19, for each participant, and performed a Fisher's exact test to rule out the possibility of the previous event being influencing memory recollection of the subsequent one.

No statistical significance was found ($p > 0.05$, two tail) which indicates that the appearance of recalled or forgotten is random and the fact that one event is recalled/forgotten doesn't mean that the next one will also be.

3.3.1 LORETA source anaysis

Because the spatial resolution of EEG is inherently poor we computed the low-resolution tomography (LORETA) estimates of the neural current source distributions to find possible source

	Recalled	Forgotten	Total
Recalled	a	b	a+b
Forgotten	c	d	c+d
Total	a+c	b+d	37

FIGURE 3.19: Representative example of how contingency tables were constructed for each participant. The first colum represents the events recalled and forgotten that were following a recalled event. The second colum represents the events recalled and forgotten that were following a forgotten event.

activations that could explain the ERPs difference between recalled and forgotten events after the boundaries.

The analysis returns as possible sources of major difference in activity between recalled and forgotten events, during the N400 period, a number of different regions such as the medial prefrontal cortex or parahippocampal gyrus, Figure 3.20. The regions found are also very similar to regions found in the Chen *et al.* (2017) and Baldassano *et al.* (2017) papers [22], [29]. Our source analysis is also in accordance to convergent evidence supporting these areas as sources of N400 activity [60]–[62].

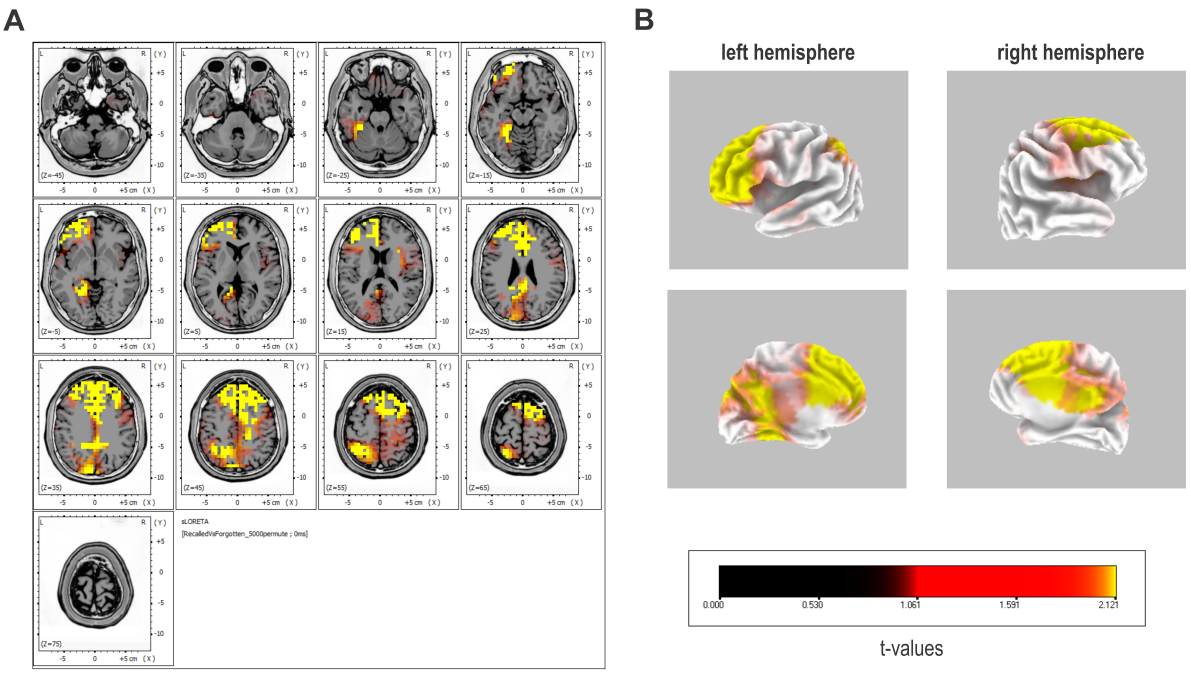

FIGURE 3.20: (A) Representative brain slices with the activated areas depicted. (B) 3D brain projection of the left and right hemisphere with the activated areas depicted.

4 Discussion

Our results provide the first electrophysiological evidence for a memory related electrophysiological signature of the event segmentation process. We found that, when facing a naturalistic continuous stimuli, our brain perceives the information in the form of discrete events which are stored in memory during a process that seems to occur approximately 400 ms after the end of each event. This study followed previous work from Chen *et al.* (2017) and Baldassano *et al.* (2017) [22], [29], in which the same experimental design was applied. However, in this project we choose to record brain activity using electroencephalography instead of fMRI so that we could gain temporal resolution and study the dynamics of memory formation during the event segmentation process. The application of this type of measurement proved to be fruitful and our results suggest that electrophysiological techniques could and should be used in the future to further investigate the memory storage and reinstatement that seems to be present during event segmentation.

EEG activity is most sensitive to a particular set of postsynaptic potentials: those generated in superficial layers of the cortex, on the crests of gyri directly next and radial to the skull. Since the EEG activity picked up on the experiment would come from mostly higher order regions, we expected to find a movie segmentation similar to the one performed by higher order regions in Baldassano *et al.* (2017) [22]. In his work boundaries annotated by human observers were strongly related to boundaries identified in higher order regions, such as the posterior medial cortex and the angular gyrus, so in our work we started by constructing a model based on the human annotations of six external participants to check if our data could be segmented in the same number of events. The constructed model fitted quite well to the data at the group level ($p < 0.05$, two tail) which confirms that the brain signal recorded using EEG is indeed capturing meaningful information from the movie while segmenting it in a way similar to the human annotations. We also expected the data from the verbal recalls to be reinstated in the same matter as it was encoded, *e.g.* in the form of events. Because the data seemed to be encoded in a similar manner as the human annotations we could expect the recall data to also show a similar segmentation pattern. However, we did not find a significance at the group level ($p > 0.05$, two tailed) which can, nevertheless, be explained by the fact that most probably some of the events encoded during the stimuli presentation were latter forgotten. Also, given that participants describe differently the events, some taking longer than others, it might also explain why the events from the human annotations model didn't fit well the recall data.

Another way to test if encoding and recall are being processed similarly is to check if the

neural patterns during encoding are similar to the ones during recall. But first it is important to check if the patterns are similar across participants during both processes. As in the Chen *et al.* (2017) paper [29] we found shared neural representations of real-world events across participants both during movie viewing, as expected since participants were facing similar stimuli [55], and during free verbal and unguided recall, where participants report the events in different ways and taking different time. However, when comparing the encoding patterns to the recollection patterns we found no statistical similarity ($p > 0.05$, two tailed) which again, could be explained by the fact that the human annotations model did not fit well to the neurophysiological data.

The fact that the human annotations model did not seem to capture well the event segmentation process during recall does not mean that, during recollection, information is not being reinstated in the form of events. To address the subjectiveness of the verbal recall we used a data-driven event segmentation algorithm, developed and applied in Baldassano *et al.* (2017) [22], which returns the most probable division of a given signal in a certain number of events, to assess if we could find the movie event patterns without any temporal constraints. Using this approach we were able to return the best segmentation of the 38 events for each particular participant and, in doing so, find similar encoding and recollection patterns such as in the Chen *et al.* (2017) and Baldassano *et al.* (2017) papers [22], [29].

The just described analysis served to prove that we could indeed use EEG data to unravel similar results to the previous papers and ensure that our data contained information about the segmentation process that is performed by the brain. We proved that neural representations with the shape of events were formed in a systematic manner across different participants. These representations undergo a transformation process between perception and recall that reveals a shared memory trace given that the neural representations remain similar to encoding, across participants, during recollection. However, thus far we could not be sure about where the memory encoding process initiated. If it was while perceiving the event (online process) or after the end of the it (offline process). To rule out the first possibility, we performed point biserial correlations between the within event correlations and a dichotomous variable where 1 meant that an event was later reported during verbal recall, and 0 that wasn't, and linear regression analysis to see if memory accuracy was correlated with temporal order, temporal length or level of details of each event. Only temporal length revealed to be significant ($p < 0.05$, two tailed), so in our next steps we tried to evaluate the second possibility.

The *Event Segmentation Theory* [12] refers to boundaries as spikes in prediction error that affect not only our perception of the just experienced information but also our expectations to what might happen in the immediate future. These predictions are essential for long-term organization, such that elements within event can be bound together cohesively. Thus, event boundaries are strong candidates as mediators of memory consolidation during naturalistic experience. The first prove of this link was found by Ben-Yakov *et al.* (2011) [24]. His research showed that brain-activity, acquired with fMRI, time-locked to the offset of narrative episodes,

occurring in a set of regions including the hippocampus, was correlated with subsequent memory performance. The hippocampus is known to play an important role in episodic memory formation [3] so, the fact that its activity is triggered by activity at event boundaries [22]–[25], proposes that some memory consolidation of just encoded events occurs at the boundary level which leads to the registration of the event into long-term memory. Given so, in this project we hypothesized that the brain activity time-locked to a boundary could be predictive of later reinstatement of that specific event. Our ERPs analysis revealed a statistically significant difference ($p < 0.05$, two tailed) between recalled and forgotten events (preceding each boundary) arising approximately 400ms after the onset of the boundary confirming our hypothesis, a value within the range found in Sols *et al.* (2017) [26] for memory reinstatement at the boundary level. The activity linked to the recalled events demonstrated a negative-going voltage occurring approximately 400 ms after the boundary onset which corresponds to the N400 component. This component has been previously linked to the semantic integration of a given stimulus into a previous context, *e.g.* the more incongruent the new context is the more prominent the N400 activity [57]–[59]. The difference between recall and forgotten was also tested on a cluster permutation analysis which revealed a cluster of significant values ($p < 0.05$, one tail) around the period of the N400 appearance. To rule out the possibility that the N400 activity was related to the event after the boundary, the same ERPs were computed considering as forgotten/recalled the events following each boundary. No difference was found between the two ($p > 0.05$, two tailed) and there was no presence of a N400 activity type. This imply that the N400 activity found is indeed predictive of later recollection when considering the activity on the offset of each event.

A spatiotemporal similarity pattern analysis (STPS) revealed that, as suggested by the *Event Segmentation Theory* [12], feature alterations during perception result in an anti-correlation between the previous and the new event information. This boundary effect could also be observed in the within and between event similarity spatiotemporal maps, were we found high similarity values within events and high dissimilarity between the two events, which confirms that the negative correlation between two events could not just be explained by spatiotemporal distances between them.

The presence of the N400 component and the results of the STPS analysis speak about the possible prediction error mechanism that occurs at each event boundary. Novelty has been suggested as an important factor in learning. For example, people tend to remember better an item that deviated from its prevailing context (incongruency), a theory called predictive coding models of memory in which the key factor that drives learning is the amount of prediction error [63]. In the context of this study one could propose that, when there's a context shift in an event, because of the incongruence between the previous and the new event, a transient increase in prediction error occurs [12]. This prediction error shift results in a hippocampus activity activation which triggers it to register the just encoded event in long-term memory [22]–[25]. Despite the low spatial resolution of EEG, our source analysis suggests some activation of the MTL during the N400 period which might suggest some hippocampal activation. Our analysis also suggests

the involvement of other memory related regions such as the medial prefrontal cortex (mPFC). The interaction between the MTL and mPFC has been suggested to play an important role in successful encoding and retrieval [64]–[66]. A new framework called SLIMM (schema-linked interactions between prefrontal and medial temporal regions) suggests that during encoding and replay, mPFC activity detects the congruence of new experiences with previous existent information and inhibits the MTL, which has been shown to automatically capture new experiences [67], from biding the information as a new instance, e.g. the more congruent a new information is the more mPFC-MTL coupling. Better schematic memory for congruent items will then be mediated by the mPFC and better instance memory for incongruent items by the MTL. The presence of these two regions in our source analysis suggests that, after the end of an event, a congruent/incongruent evaluation might take place, marked by the N400 appearance, which results in a mPFC-MTL interaction that, by itself, leads to a successful encoding and later recollection of the event. However, given that our source analysis suggests only possible activated regions, the mPFC-MTL role at event segmentation can only be seen as a possible explanation for memory performance, and future research would be needed to test this hypothesis.

4.1 Study Limitations

The major limitation of this study arises from the nature of the experimental design. By asking participants to watch a movie for 50 min without breaks we ended up facing problems of attention and sleepiness, having to discard two participants for falling asleep. The duration of the movie also results in a bigger number of movement artifacts, given that participants cannot stay still for such long time and when getting sleepy tend to move to force themselves to stay awake. The free verbal recall nature of the task also contributed greatly to the rise of noise in this part of the data due to the fact that the EEG signal is very sensitive to the facial movements of participants talking. For all of this reason, in this study, we were sometimes faced with challenging data from the amount of noise point of you, forcing us to take measures such as filtering a great number of frequencies or smooth the data, which might have resulted in the elimination of some meaningful signal dynamics. We can also say that the choice of movie might not have been the best one given that, in the first minutes of the movie, the transitions between scenes are very fast which probably does not happen in lifelike experience. Given that, one of the main objectives of this project was to use a more ecological stimulus, which more closely approximated to real life, perhaps another movie with less abrupt transitions should have been used. An alternative would have been to perhaps show more that one movie so that we could assess if our results can be generalized to other types of visual stimuli. Nevertheless, this particular movie was chosen because it had already been used in a number of previous studies related with event segmentation [22], [29] and so that we could compare our results with this given papers.

The low spatial resolution of the EEG was also a limitation of this study and the sources of activity suggested in the discussion can not be seen as more than predictions. However, our main goal in using EEG was to gain temporal resolution so that we could provide insights into the brain dynamics during the event segmentation process, which hadn't been studied until now.

Finally, we expected to make more use of the data-driven event segmentation algorithm than we did in the end. By doing so we would have had more objectiveness in our results, because the boundaries could have been extracted directly from the data instead of having to rely on external participant's annotations. Unfortunately, when asking the model to search freely for a certain number of patterns, the model didn't provide a clear distinction of scenes, perhaps because of the amount of noise in the data. Given so, we were only able to use the model when asking it to search for the mean movie patterns of the human annotations model on the recall data, which by itself already removes part of the data-driven advantage of this algorithm.

5 Conclusions

All in all, our results provide further electrophysiological evidence for the importance of memory consolidation at event boundaries as a way to bridge temporally adjacent events during encoding, while storing them as cohesive units of schema related information. Following previous work [22], [23], [26], [29] we demonstrate that the brain perceives the information that arrives to us in our daily-life experience in the form of discrete events which are stored in memory during a process that occurs approximately 400 ms after the end of each event and that is predictive of latter reinstatement.

There has been a growing interest on the neural basis of memory during real-life experience and so, in using a more naturalistic experimental design, our results testify to the robustness and ecological validity of the uncovered neural dynamics. We proved that naturalistic stimulus can be used in electroencephalography measurements, despite the natural limitations that arise with the use of such stimuli, such as the increase in movement artifacts or tendency to sleepiness.

Our results suggest a possible congruency/incongruency evaluation mechanism as part of the event segmentation process. This mechanism might represent the error-based updating mechanism, in which event models are updated at event boundaries in response to transient increases in prediction error, suggested by the *Event Segmentation Theory*.

The overall results shine a light into the understanding of the neural dynamics of memory formation during event segmentation of naturalistic continuous stimuli. Nevertheless, future research is needed to test the relevance of the novelty evaluation mechanism proposed in this work and if it is indeed fundamental not only for correct memory formation of an event but also for binding temporal adjacent events and consequent returning of the general schema of an experience. It is also in our opinion that future research should push for more naturalistic experimental designs, such as making use of life recordings with electrocorticography (ECoG), that although more invasive and only applied in patients could provide us with less noisy data while keeping the temporal resolution, and more data-driven methods, as the event segmentation model applied in this work, to truly validate the results and unravel the true nature of the event segmentation mechanisms, which have proven to play an essential role in the construction of episodic memories.

Bibliography

[1] R. K. Lech, *The integration of memory and visual perception in the human medial temporal lobe*, 2014.

[2] W. B. Scoville and B. Milner, "Loss of recent memory after bilateral hippocampal lesions.", *Journal of neurology, neurosurgery, and psychiatry*, vol. 20, no. 1, pp. 11–21, 1957, ISSN: 0022-3050.

[3] L. R. Squire and S Zola-Morgan, "The medial temporal lobe memory system.", *Science (New York, N.Y.)*, vol. 253, no. 5026, pp. 1380–6, 1991, ISSN: 0036-8075.

[4] J. P. Aggleton and M. W. Brown, "Episodic memory, amnesia, and the hippocampal anterior thalamic axis.", *The Behavioral and brain sciences*, vol. 22, no. 3, 425–44; discussion 444–89, 1999, ISSN: 0140-525X.

[5] J. S. Simons and H. J. Spiers, "Prefrontal and medial temporal lobe interactions in long-term memory", *Nature Reviews Neuroscience*, vol. 4, no. 8, pp. 637–648, 2003, ISSN: 1471-003X.

[6] S. Cansino, P. Maquet, R. J. Dolan, and M. D. Rugg, "Brain activity underlying encoding and retrieval of source memory.", *Cerebral cortex (New York, N.Y. : 1991)*, vol. 12, no. 10, pp. 1048–56, 2002, ISSN: 1047-3211.

[7] D Marr, "Simple memory: a theory for archicortex.", *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, vol. 262, no. 841, pp. 23–81, 1971, ISSN: 0962-8436.

[8] A. C. Schapiro, N. B. Turk-Browne, M. M. Botvinick, and K. A. Norman, "Complementary learning systems within the hippocampus: a neural network modelling approach to reconciling episodic memory with statistical learning", *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 372, no. 1711, p. 20 160 049, 2017, ISSN: 0962-8436.

[9] L. R. Squire and S Zola-Morgan, "Memory: brain systems and behavior.", *Trends in neurosciences*, vol. 11, no. 4, pp. 170–5, 1988, ISSN: 0166-2236.

[10] N. J. Cohen and L. R. Squire, "Preserved learning and retention of pattern-analyzing skill in amnesia: dissociation of knowing how and knowing that.", *Science (New York, N.Y.)*, vol. 210, no. 4466, pp. 207–10, 1980, ISSN: 0036-8075.

[11] J. M. Zacks, T. S. Braver, M. A. Sheridan, D. I. Donaldson, A. Z. Snyder, J. M. Ollinger, R. L. Buckner, and M. E. Raichle, "Human brain activity time-locked to perceptual event boundaries", *Nature Neuroscience*, vol. 4, no. 6, pp. 651–655, 2001, ISSN: 1097-6256.

[12] J. M. Zacks, N. K. Speer, K. M. Swallow, T. S. Braver, and J. R. Reynolds, "Event perception: a mind-brain perspective.", *Psychological Bulletin*, vol. 133, no. 2, pp. 273–293, 2007, ISSN: 1939-1455.

[13] A. C. Schapiro, T. T. Rogers, N. I. Cordova, N. B. Turk-Browne, and M. M. Botvinick, "Neural representations of events arise from temporal community structure", *Nature Neuroscience*, vol. 16, no. 4, pp. 486–492, 2013, ISSN: 1097-6256.

[14] L. L. Richmond and J. M. Zacks, "Constructing experience: event models from perception to action", *Trends in Cognitive Sciences*, vol. 21, no. 12, pp. 962–980, 2017, ISSN: 13646613.

[15] J. Q. Sargent, J. M. Zacks, D. Z. Hambrick, R. T. Zacks, C. A. Kurby, H. R. Bailey, M. L. Eisenberg, and T. M. Beck, "Event segmentation ability uniquely predicts event memory", *Cognition*, vol. 129, no. 2, pp. 241–255, 2013, ISSN: 00100277.

[16] J. M. Zacks, B Tversky, and G Iyer, "Perceiving, remembering, and communicating structure in events.", *Journal of experimental psychology. General*, vol. 130, no. 1, pp. 29–58, 2001, ISSN: 0096-3445.

[17] U. Hasson, E. Yang, I. Vallines, D. J. Heeger, and N. Rubin, "A hierarchy of temporal receptive windows in human cortex", *Journal of Neuroscience*, vol. 28, no. 10, pp. 2539–2550, 2008, ISSN: 0270-6474.

[18] Y. Lerner, C. J. Honey, L. J. Silbert, and U. Hasson, "Topographic mapping of a hierarchy of temporal receptive windows using a narrated story", *Journal of Neuroscience*, vol. 31, no. 8, pp. 2906–2915, 2011, ISSN: 0270-6474.

[19] U. Hasson, J. Chen, and C. J. Honey, "Hierarchical process memory: memory as an integral component of information processing.", *Trends in cognitive sciences*, vol. 19, no. 6, pp. 304–13, 2015, ISSN: 1879-307X.

[20] C. J. Honey, T. Thesen, T. H. Donner, L. J. Silbert, C. E. Carlson, O. Devinsky, W. K. Doyle, N. Rubin, D. J. Heeger, and U. Hasson, "Slow cortical dynamics and the accumulation of information over long timescales", *Neuron*, vol. 76, no. 2, pp. 423–434, 2012, ISSN: 08966273.

[21] G. J. Stephens, C. J. Honey, and U. Hasson, "A place for time: the spatiotemporal structure of neural dynamics during natural audition", *Journal of Neurophysiology*, vol. 110, no. 9, pp. 2019–2026, 2013, ISSN: 0022-3077.

[22] C. Baldassano, J. Chen, A. Zadbood, J. W. Pillow, U. Hasson, and K. A. Norman, "Discovering event structure in continuous narrative perception and memory", *Neuron*, vol. 95, no. 3, 709–721.e5, 2017, ISSN: 08966273.

[23] A. Ben-Yakov and R. N. Henson, "The hippocampal film-editor: sensitivity and specificity to event boundaries in continuous experience", *BioRxiv*, p. 273 409, 2018.

[24] A. Ben-Yakov and Y. Dudai, "Constructing realistic engrams: poststimulus activity of hippocampus and dorsal striatum predicts subsequent episodic memory", *Journal of Neuroscience*, vol. 31, no. 24, pp. 9032–9042, 2011, ISSN: 0270-6474.

[25] A. Ben-Yakov, N. Eshel, and Y. Dudai, "Hippocampal immediate poststimulus activity in the encoding of consecutive naturalistic episodes.", *Journal of Experimental Psychology: General*, vol. 142, no. 4, pp. 1255–1263, 2013, ISSN: 1939-2222.

[26] I. Sols, S. DuBrow, L. Davachi, and L. Fuentemilla, "Event boundaries trigger rapid memory reinstatement of the prior events to promote their representation in long-term memory.", *Current biology : CB*, vol. 27, no. 22, 3499–3504.e4, 2017, ISSN: 1879-0445.

[27] O. Jeunehomme and A. D'Argembeau, "Event segmentation and the temporal compression of experience in episodic memory", *Psychological Research*, 2018, ISSN: 0340-0727.

[28] J. Linde-Domingo, M. S. Treder, C. Kerren, and M. Wimber, "Evidence for a reversal of the neural information flow between object perception and object reconstruction from memory", *BioRxiv*, p. 300 913, 2018.

[29] J. Chen, Y. C. Leong, C. J. Honey, C. H. Yong, K. A. Norman, and U. Hasson, "Shared memories reveal shared structure in neural activity across individuals", *Nature Neuroscience*, vol. 20, no. 1, pp. 115–125, 2017, ISSN: 1097-6256.

[30] F Mechler, J. D. Victor, K. P. Purpura, and R Shapley, "Robust temporal coding of contrast by v1 neurons for transient but not for steady-state stimuli.", *The Journal of neuroscience : The official journal of the Society for Neuroscience*, vol. 18, no. 16, pp. 6583–98, 1998, ISSN: 0270-6474.

[31] H. Yao, L. Shi, F. Han, H. Gao, and Y. Dan, "Rapid learning in cortical coding of visual scenes", *Nature Neuroscience*, vol. 10, no. 6, pp. 772–778, 2007, ISSN: 1097-6256.

[32] A. Belitski, A. Gretton, C. Magri, Y. Murayama, M. A. Montemurro, N. K. Logothetis, and S. Panzeri, "Low-frequency local field potentials and spikes in primary visual cortex convey independent visual information", *Journal of Neuroscience*, vol. 28, no. 22, pp. 5696–5709, 2008, ISSN: 0270-6474.

[33] D. H. Brainard, "The psychophysics toolbox.", *Spatial vision*, vol. 10, no. 4, pp. 433–6, 1997, ISSN: 0169-1015.

[34] D. G. Pelli, "The videotoolbox software for visual psychophysics: transforming numbers into movies.", *Spatial vision*, vol. 10, no. 4, pp. 437–42, 1997, ISSN: 0169-1015.

[35] M Kleiner, D Brainard, D. Pelli, A Ingling, R Murray, and C Broussard, *What's new in psychtoolbox-3*, 14. [Pion Ltd.], 2007, vol. 36, pp. 1–16.

[36] *Psychology software tools, inc. [e-prime 2.0].* 2012.

[37] A. Delorme and S. Makeig, "Eeglab: an open source toolbox for analysis of single-trial eeg dynamics including independent component analysis", *Journal of Neuroscience Methods*, vol. 134, no. 1, pp. 9–21, 2004, ISSN: 01650270.

[38] A. Pérez, M. Carreiras, and J. A. Duñabeitia, "Brain-to-brain entrainment: eeg interbrain synchronization while speaking and listening", *Scientific Reports*, vol. 7, no. 1, p. 4190, 2017, ISSN: 2045-2322.

[39] B. Levine, E. Svoboda, J. F. Hay, G. Winocur, and M. Moscovitch, "Aging and autobiographical memory: dissociating episodic from semantic retrieval.", *Psychology and aging*, vol. 17, no. 4, pp. 677–89, 2002, ISSN: 0882-7974.

[40] U. Hasson, Y. Nir, I. Levy, G. Fuhrmann, and R. Malach, "Intersubject synchronization of cortical activity during natural vision.", *Science (New York, N.Y.)*, vol. 303, no. 5664, pp. 1634–40, 2004, ISSN: 1095-9203.

[41] U. Hasson, R. Malach, and D. J. Heeger, "Reliability of cortical activity during natural stimulation.", *Trends in cognitive sciences*, vol. 14, no. 1, pp. 40–8, 2010, ISSN: 1879-307X.

[42] J. R. Anderson, H. S. Lee, and J. M. Fincham, "Discovering the structure of mathematical problem solving", *NeuroImage*, vol. 97, pp. 163–177, 2014, ISSN: 1053-8119.

[43] A. P. Baker, M. J. Brookes, I. A. Rezek, S. M. Smith, T. Behrens, P. J. Probert Smith, and M. Woolrich, "Fast transient networks in spontaneous human brain activity", *ELife*, vol. 3, 2014, ISSN: 2050-084X.

[44] T. Rukat, A. Baker, A. Quinn, and M. Woolrich, "Resting state brain networks from eeg: hidden markov states vs. classical microstates", 2016. arXiv: 1606.02344.

[45] L. E. Baum and T. Petrie, "Statistical inference for probabilistic functions of finite state markov chains", *The Annals of Mathematical Statistics*, vol. 37, no. 6, pp. 1554–1563, 1966, ISSN: 0003-4851.

[46] L. E. Baum and J. A. Eagon, "An inequality with applications to statistical estimation for probabilistic functions of markov processes and to a model for ecology", *Bulletin of the American Mathematical Society*, vol. 73, no. 3, pp. 360–364, 1967, ISSN: 0002-9904.

[47] L. E. Baum, T. Petrie, G. Soules, and N. Weiss, "A maximization technique occurring in the statistical analysis of probabilistic functions of markov chains", *The Annals of Mathematical Statistics*, vol. 41, no. 1, pp. 164–171, 1970, ISSN: 0003-4851.

[48] L. Rabiner, "A tutorial on hidden markov models and selected applications in speech recognition", *Proceedings of the IEEE*, vol. 77, no. 2, pp. 257–286, 1989, ISSN: 00189219.

[49] N. Kriegeskorte and R. A. Kievit, "Representational geometry: integrating cognition, computation, and the brain.", *Trends in cognitive sciences*, vol. 17, no. 8, pp. 401–12, 2013, ISSN: 1879-307X.

[50] S. J. Luck, *An introduction to the event-related potential technique*, p. 406, ISBN: 9780262525855.

[51] R. Oostenveld, P. Fries, E. Maris, and J.-M. Schoffelen, "Fieldtrip: open source software for advanced analysis of meg, eeg, and invasive electrophysiological data.", *Computational intelligence and neuroscience*, vol. 2011, p. 156 869, 2011, ISSN: 1687-5273.

[52] R. D. Pascual-Marqui, "Standardized low-resolution brain electromagnetic tomography (sloreta): technical details.", *Methods and findings in experimental and clinical pharmacology*, vol. 24 Suppl D, pp. 5–12, 2002, ISSN: 0379-0355.

[53] M. Fuchs, J. Kastner, M. Wagner, S. Hawes, and J. S. Ebersole, "A standardized boundary element method volume conductor model.", *Clinical neurophysiology : Official journal of the International Federation of Clinical Neurophysiology*, vol. 113, no. 5, pp. 702–12, 2002, ISSN: 1388-2457.

[54] V. Jurcak, D. Tsuzuki, and I. Dan, "10/20, 10/10, and 10/5 systems revisited: their validity as relative head-surface-based positioning systems", *NeuroImage*, vol. 34, no. 4, pp. 1600–1611, 2007, ISSN: 10538119.

[55] C. A. Kurby and J. M. Zacks, "Segmentation in the perception and memory of events.", *Trends in cognitive sciences*, vol. 12, no. 2, pp. 72–9, 2008, ISSN: 1364-6613.

[56] M. Nguyen, T. Vanderwal, and U. Hasson, "Shared understanding is correlated with shared neural responses in the default mode network", *BioRxiv*, p. 231 019, 2017.

[57] M Kutas and S. A. Hillyard, "Reading senseless sentences: brain potentials reflect semantic incongruity.", *Science (New York, N.Y.)*, vol. 207, no. 4427, pp. 203–5, 1980, ISSN: 0036-8075.

[58] W. B. McPherson and P. J. Holcomb, "An electrophysiological investigation of semantic priming with pictures of real objects.", *Psychophysiology*, vol. 36, no. 1, pp. 53–65, 1999, ISSN: 0048-5772.

[59] T. Sitnikova, G. Kuperberg, and P. J. Holcomb, "Semantic integration in videos of real-world events: an electrophysiological investigation.", *Psychophysiology*, vol. 40, no. 1, pp. 160–4, 2003, ISSN: 0048-5772.

[60] E. Halgren, R. P. Dhond, N. Christensen, C. Van Petten, K. Marinkovic, J. D. Lewine, and A. M. Dale, "N400-like magnetoencephalography responses modulated by semantic context, word frequency, and lexical class in sentences.", *NeuroImage*, vol. 17, no. 3, pp. 1101–16, 2002, ISSN: 1053-8119.

[61] A. M. Proverbio, F. Riva, and A. Zani, "When neurons do not mirror the agent's intentions: sex differences in neural coding of goal-directed actions", *Neuropsychologia*, vol. 48, no. 5, pp. 1454–1463, 2010, ISSN: 00283932.

[62] A. Ibáñez, J. F. Cardona, Y. V. Dos Santos, A. Blenkmann, P. Aravena, M. Roca, E. Hurtado, M. Nerguizian, L. Amoruso, G. Gómez-Arévalo, A. Chade, A. Dubrovsky, O. Gershanik, S. Kochen, A. Glenberg, F. Manes, and T. Bekinschtein, "Motor-language coupling: direct evidence from early parkinson's disease and intracranial cortical recordings", *Cortex*, vol. 49, no. 4, pp. 968–984, 2013, ISSN: 00109452.

[63] R. N. Henson and P. Gagnepain, "Predictive, interactive multiple memory systems", *Hippocampus*, vol. 20, no. 11, pp. 1315–1326, 2010, ISSN: 10509631.

[64] C. Ranganath, A. Heller, M. X. Cohen, C. J. Brozinsky, and J. Rissman, "Functional connectivity with the hippocampus during successful memory formation", *Hippocampus*, vol. 15, no. 8, pp. 997–1005, 2005, ISSN: 1050-9631.

[65] A. Peyrache, M. Khamassi, K. Benchenane, S. I. Wiener, and F. P. Battaglia, "Replay of rule-learning related neural patterns in the prefrontal cortex during sleep", *Nature Neuroscience*, vol. 12, no. 7, pp. 919–926, 2009, ISSN: 1097-6256.

[66] K. Benchenane, A. Peyrache, M. Khamassi, P. L. Tierney, Y. Gioanni, F. P. Battaglia, and S. I. Wiener, "Coherent theta oscillations and reorganization of spike timing in the hippocampal- prefrontal network upon learning", *Neuron*, vol. 66, no. 6, pp. 921–936, 2010, ISSN: 08966273.

[67] M. Moscovitch, "The hippocampus as a "stupid," domain-specific module: implications for theories of recent and remote memory, and of imagination.", *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale*, vol. 62, no. 1, pp. 62–79, 2008, ISSN: 1878-7290.